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ORGANIC RESPONSE[1]

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AT no time in the history of natural science has such a large share of thought and research energy been directed to the solution of evolutionary problems as at present. Methods of work, plans for experimentation and modes of interpretation have recently undergone such rapid development and improvement that our potentiality for solving questions in heredity and origination is vastly greater than even at such recent date as the beginning of this new century. With increased facility in attack has also come wider vision and altered viewpoints with regard to almost all phases of biology.

Biological thought once quickened and broadened by evolutionary ideas was by this same means led to become entangled in a maze of illusive assumptions as to purpose and plan in organisms from which it is being but slowly freed, to view functions as inevitable reactions, however complex they may be. The variables included in the equations of protoplasmic action are numerous and large, but they do not exceed the undefined principles of osmotic action, surface tension and unknown phases of association and dissociation that are concerned in the interplay of substances in the cell, and upon which

[1] Presidential address, Society of American Naturalists, Ithaca, New York, December 29, 1910.

depend the chemico-physical relations of tissue components and structures of all kinds. If physiology escapes the soporific and deadening influence of the vitalistic conceptions, now appearing in some profusion, it may in turn furnish the secure means for a long and rapid advance in genetics, and it may be assumed with some certainty that the chief superstructures of evolutionary science will be those securely raised upon a foundation of physiologically tested facts.

In taking this direction, natural history is not alone; the briefest comprehensive view of the physical sciences will show that here also the chief advance lies along the way of the study of energetics, and that the fundamental problems are those lying about the mode and means of transformations of energy.

Recent events in the field of evolution comprehend a number of movements and accomplishments of extraordinary interest. The rediscovery of the facts of alternative inheritance, the formulation of the concepts of equivalent, balanced, paired or differential characters, the results of statistical studies of variability, the analyses of species of various constitution by pedigree cultures, in which the value of fertilization from various sources is carefully measured, the distinction of the biotype or genotype as a hereditary entity, the possibilities in the action of pure lines within a specific group, the cytological contributions of fact and forecast upon the physical aspects of heredity, and lastly the presentation of the facts and allowable generalizations identified with the mutation theory, comprise a series of advances, of accretions to knowledge, furnish a broadened foundation for biological science, and disclose additional possibilities in all lines of experimental research with living things, besides opening up new realms for speculative thought, and stimulating the scientific imagination to renewed fruitfulness.

Biological literature has also been recently enriched by a series of formal papers commemorative of the life and work of Charles Darwin, by more than fourscore workers

representing the laboratories and national cultures of the world. This group of addresses and essays, fortunately written chiefly within four languages, taken collectively, constitutes a critical and evaluatory discussion of the mass of fact and galaxy of theory concerning organic evolution, and furnishes the most complete and thorough appraisal ever made of any subject in modern biology.

The moment, therefore, is one of consciousness of achievement, of realization of increased powers of penetration, and charged with desire for the exploitation of the unknown, and is vibrant with the inspiration coming from such a rapid march of events. With this quickening in activity, the outcries of acrid controversies no longer monopolize our attention, but it must not be supposed that differences of opinion have vanished from among us. The agreement as to the value of methods of experimentation and calibration is a most gratifying fact, but the harmonies of opinion as to interpretation of results have not yet come to a monotone.

On the contrary, the pressure of new and undisciplined evidence has awakened a freshened chorus of voices crying the virtues of special interests and extolling the sufficiency of theories dignified by age and more or less weighty with authority. Those busy with vitalism of various patterns have spun a moiety of their favorite fabric to mend the breaks in the fragile web made by the impact of new facts. Isolation and the mechanism of geographical distribution have again been elaborated to account for all differentiation and what their exponents are pleased to term speciation. The anticipatory formation of structures in a rudimentary condition with a long prefunctional progress, guided by the morphological possibilities and actuated by internal impulses, has again been offered to us, fortified by paleontological fact and clever logic, in such manner as to avoid most of the serious objections to orthogenesis except those of physiological morphology.

Natural selection with diverse meanings and manifold implications has been made to explain development, differentiation and general evolutionary progress. The tumult is greatest at the present time, however, about the idea of mutation. Standing to one side, the biologist hears a medley of assertions "that mutations have long been known," "do not exist," "were discovered by Darwin," "are always an evidence of hybridization," "result in the formation of nothing but elementary species," "give only weakened derivatives that are quickly swamped by parental forms," "are encountered only among cultivated plants," "the mutation theory is based upon the conception of unit characters," "constitutes the only adequate means of accounting for the enormous number of living forms and myriad characters of living things," "unit characters are unreal, have never been seen, do not exist and are incapable of demonstration." "The difference between mutation and variation is one of amplitude only," and lastly mutation signally "refutes Darwinism," and "swings us back in harmony with the theologian's arguments for special creation."

The absurdity of the many injudicial assertions by the partisans concerned need not blind us to the stubborn fact that saltatory changes do occur in hereditary pure lines in a large number of forms in both plants and animals. Observations and experiments have established beyond doubt that mutation is one way by which organisms bearing new combinations of qualities may arise, although it is probable that its importance as a general procedure varies in different groups of organisms and certain that many shades of opinion as to its exact part in the evolution of living things will always be held.

Our appraisement of the value of all the protheses cited may also be amended from time to time with viewpoints altered by the advance of knowledge. The situation with regard to one hypothesis is far more serious, however. This is the theory which predicates direct adaptational adjustment of the organism, quickly or

slowly as the case may be, to environic factors, and the inheritance of the somatic alterations constituting such variations. The various corollaries of this theory have the force of a certain obviousness, its assumptions have been of ready service to the systematist and biogeographer, and its conclusions have long been tolerated in the absence of decisive tests which are not to be easily made or readily carried out. The time has now arrived, however, when the claimants for Neo-Lamarckianism and all of its conclusions must show cause for its further consideration, or else allow it to drop from the position of being seriously taken as a method of evolutionary advance.

It is unanimously agreed that organisms, plants as well as animals, change individually in aspect, in form and structure of organs, in functionation and habit as they encounter swamps, saline areas, gravelly uplands or slopes, climatic differences identifiable with latitude or elevation, and other physical and biological factors. It is assumed that these somatic alterations are accommodative and adaptive, making the organism more suitable for the conditions which produce the changes. Such an assumption is an over-reaching one. Any analysis of the changes which an organism undergoes after transportation to a new habitat will disclose one or a few alterations which might be of advantage in dealing with the newly encountered conditions, but with these are many others, direct, necessitous, atrophic, or hypertrophic as to organs which have no relation whatever to usefulness or fitness. Further, a critical examination fails to disclose any theoretical considerations or any actual facts which would connect inevitably the somatic response with the nature of the excitation, outside of the specialized tropisms in which specific reactions are displayed. Even in these the adjustment is of such nature that a mechanism specially perceptive to contact, for example, may react to changes in temperature, as illustrated by the action of tendrils, and many similar cases might be cited. It is evident that the soma of a plant or animal is not to be

considered as capable of adaptive alterations to every new agency which may cause changes in its form, structure or functionation.

Next we come to the very crux of the whole matter: do the unusual forms or activities of organs resulting from environic causes act in any manner upon the germ-plasm connected with such altered bodies? If we are to consider the activities of the organism or of the cell to depend mainly upon its chemical structure and constituency and such a generalization seems unavoidable, then we have means by which the soma might cause its properties to be reflected from the germ-plasm in a succeeding generation, since the chemical mechanism of the soma and germ-plasm must be of the most intimate nature. That some such connection does actually exist is strongly suggested by the behavior of a great number of organisms which have been seen to carry marked environic effects to the second or even third generations; if the interrogation be made as to why the induced qualities are carried no further it may be said that the reply may be suggested by the results of long-continued action of the exciting agency, such as has been used by Woltereck with *Daphnia*.

If a general view be taken of the available information of interest in this connection, three classes of facts will be discerned. One group is comprised in the mass of information obtained by the operations of the horticulturist, the agriculturist and the breeder as to the behavior of crops, plants and domestic animals, when transferred from one habitat to another. The greater part of such data is the result of observations which do not comply with the ordinary requirements in the avoidance of error so that strict comparisons as to the behavior of organisms under conditions of various habitats are impossible. A consideration of the literature yields many suggestions for experimental research and the simple generalization that the direct effects of climatic complexes on the seasonal cycle, and upon color, or struc-

tural features of the individual, may be repeated or carried over two or three generations, in a habitat where the specific causal combinations are lacking. This is the available total of knowledge furnished us by economic operations, and by the introduction operations of botanical gardens and plantations.

In contrast with these the fortunate experience of Zederbauer with *Capsella* has yielded some conclusions of exceptional importance. A genotype of *Capsella Bursa-pastoris* resembling *taraxicafolium* was found on the lower plains of Asia Minor, and displayed the well-known characters of this form, including broad leaves, whitish flowers, and stems 30–40 cm. high. A highway leads from these regions to a plateau at an elevation of 2,000 to 2,400 meters. The conditions of distribution are such as to indicate that the plant has been carried up this thoroughfare by man, and in this elevated habitat it has taken on certain alpine characters, including elongated roots, xerophytic leaves, stems 2–5 cm. high, reddish flowers, with a noticeable increase of the hairiness of the entire plant. That the distributional history has been correctly apprehended seems entirely confirmed by the fact that when seeds are taken from the lowlands the alpine characters enumerated are displayed at once as a direct somatic response. When seeds are taken from plants on the elevated plateau where their ancestors may have been for many years or many centuries (perhaps as long as 2,000 years) and sowed at Vienna and in other cultures carried through four generations the leaves lose their xerophytic form and structure, but the other characters are retained within the limits of variability. The stems show an increase in average length of 1 or 2 cm., the roots change as much, but the reproductive branches and floral organs retain their alpine characters. The slight modifications undergone by these features were seen to reach a maximum and to decrease in the latest generations cultivated. The structural changes and implied functional accommodations are indubitably direct

somatic responses, there is no escape from the conclusion that the impress of the alpine climate on the soma has been communicated to the germ-plasm directly or indirectly in such manner as to be transmissible, and the suggestion lies near that repeated and continued excitation by climatic factors may have been the essential factor in such fixation.[2]

Among the most noteworthy investigations of the features of interest in connection with habitat changes are those being made by the anthropologist in which somatic calibrations of immigrating races and linguistic studies of peoples of known origin, geographical movement, and established relationship are being used to great advantage. No more fascinating chapters of scientific literature are to be found than those which delineate the migratory movements, segregation and habital reactions of Polynesian islanders, of North American Indians, or of Asiatic peoples, yet their value as actual contributions to the phase of biology of interest to this society is hardly recognized. The investigator of problems in anthropology has the advantage of dealing with an animal whose psychology, history, traditions and records are readily intelligible to him, so that a much wider range of facts may be brought within the zone of reliability than when we deal with an organism whose actions, at best, are but imperfectly understood by us.[3]

A second series of results of great interest and suggestiveness are those which have been obtained in various laboratories as to the individual modifications in cyclical activity, functionation and structure of plants and animals in response to unusual stimuli, or under the influence of unusual intensities of the common environic components. The behavior of organisms in constant illumination, equable and variable temperatures, salinity, alkalinity or acidity of the medium, unusual pressures of at-

[2] "Versuche ueber Vererbung erworbener Eigenschaften bei *Capsella bursa pastoris*," *Oester. Bot. Zeitschr.*, Vol. 58: pp. 231–236, 285–288, 1908.

[3] See Boas, F., "Changes in Bodily Form of Descendants of Immigrants," The Immigration Committee, Document No. 208, presented to the 61st Congress, 2d Session, Washington, D. C., U. S. A., 1910.

nospheric constituents, to unusual compounds and unaccustomed food-material, make up an important proportion of the sum total of information ordinarily classified as physiology. The morphogenic and accommodative adjustments presented afford by analysis the best conceptions available as to the nature of the physiologic activity of organisms.

The experimental results of Stockard with fish eggs subjected to the action of various chemical substances are of unusual interest in the present connection. The cyclopean embryos of *Fundulus* formed in sea-water containing magnesium salts offer the first known example of the induction of an abnormality in the vertebrates occurring in nature, by specific reagents. Suggestion of a common cause is obvious as it is in the instances in which similar divergences have been secured in the laboratory with plants. As will be pointed out later, such analytical tests constitute a very important part of the procedure in the study of acclimatization results.[4]

In very few cases, however, has the permanency or heritability of the deviations induced been tested, and in most of such tests the agencies employed might have acted upon both soma and germ-plasm, as will be apparent upon an examination of the work of Standfuss, Fischer, Pictet and Houssey. The work of these older experimenters has been reviewed so many times that it will be unnecessary to discuss their results further in the present paper. This was done at the Darwin memorial meeting in 1908, and quite recently by Bourne in his address before Section of Zoology of the British Association for the Advancement of Science, at the Sheffield meeting.[5]

The present opportunity may well be used to make a presentation of the results of the last few years obtained

[4] Stockard, C. R., "The Development of Artificially Produced Fish.—The Cyclopean Embryo," *Jour. Exper. Morphology*, Vol. 7, No. 2, p. 285, 1909.

[5] *Nature*, Vol. 84, p. 378, 1910, September 22, 1910.

by investigations, using a more perfected technique, and having the advantage of a keener insight into the real nature of the problems to be solved.

That the general hypothesis with its corollaries is being subjected to the most critical examination and that the assumptions implied in the conception of inheritance of acquired characters are being put to exact and conclusive tests, is readily apparent when a review is made of recent and current researches in which living material from widely separated groups of animals and plants is being subjected to a variety of nutritive conditions and climatic agencies. Klebs, who has long been concerned with the morphogenic reactions of plants, has determined a series of conditions under which the stages of mycelial development, asexual zoospore and sexual or oospore formations in filamentous fungi may be inhibited or variously interchanged. Much more important reactions were obtained from *Sempervivum*, the live-forever of the garden. In this plant, inflorescences were replaced by single flowers by experimental excitation while it was found the number and arrangement of the floral organs as well as of the stamens and carpels could be altered. Furthermore, the deviations in question were found to be transmissible to the second or third generation in guarded seed-reproductions.[6]

Microorganisms with a short cycle offer peculiarly advantageous material by reason of their simple reproductive processes, and also by the fact that it is possible to control environic factors with exactitude. The voluminous literature of bacteriology shows that much attention has been devoted to the building up of characters by selection, and to the study of the behavior of morphological divergences occurring in special cultures.

The experiments of Buchanan with *Streptoccus lacticus* yields the conclusion that phases of fluctuating variations in the bacteria induced by cultures may not be fixed,

[6] Alterations in the development and forms of plants as a result of environment, Proc. Roy. Soc. Lond., Vol. 82, No. B. 559, p. 547, 1910.

and are not transmissible, which is in accord with the main body of evidence upon this point. There are, however, a number of records of the appearance of definite qualities or morphological characters in the yeasts, which were transmissible and permanent. These departures were so striking as to be capable of being regarded as mutational, and their origin has been ascribed to the influence of the environment by experimenters of notable skill, such as Beijerinck, Winogradsky, Lepeschkin, Hansen and Barber. It may be recalled in this connection, that environic responses are generally sudden, and that the entire range of departure may be made in a single generation, at most in two or three.[7]

Pringsheim after a comprehensive review of his own work and of other available evidence obtained by a study of accommodations or adaptations of yeasts and bacteria to unusual temperatures, culture media, and poisons, concludes that some of these variations are fixed and transmissible both asexually and by spores, while others are not. It is not easy to analyze contributions upon this subject with reference to the differential action of the exciting agencies upon soma or germ-plasm, neither is it clear as to the action of the selection in the experimentation. It is important, however, to note that the alterations concerned are direct functional responses to the exciting agencies.[8]

The researches of Jennings with paramœcium deals with conditions of morphology and physiology not widely dissimilar from those offered by the bacteria with regard to the present problems, and his work has been carried out with an extensiveness and thoroughness impossible to the worker with more massive and more slowly moving organisms. Cultures were carried through hundreds of generations with no progressive action in fluctuating

[7] For a brief review of this subject see Buchanan, "Non-inheritance of impressed variations in *Streptoccus lacticus*," *Journal of Infectious Diseases*, Vol. 7, p. 680, 1910.

[8] Pringsheim, H., "Die Variablität niederer Organismen," Berlin, 1910.

variability; while the organism as a whole was strongly resistant to all kinds of environic influences, and actual alterations were extremely rare. Most of the supposedly acquired characters disappeared in two or three generations by fission, although one was followed for twenty-two generations. The new character was borne by only one of the pair produced by a division, except in rare instances, and in only one case was there found such modification as to produce a race bearing the odd character in which the feature in question was imperfectly transmitted in series of asexual generations.[9]

The results of Woltereck with *Daphnia* offer something by way of contrast and also serve to illustrate the necessity for continuation of parallel cultures for the purpose of comparison of divergent forms and the normal. The particular group of this crustacean furnishing the experimental material is taken to be very variable, and it was subjected to over-feeding with the immediate result that the variability of the form of the head appeared to be widened, the size of this structure being increased. This disappeared when lots from the culture were restored to normal conditions in the earlier stage of the work. After three or four months of over-feeding, the form of the head came within narrower limits, and fewer aberrants were seen, while lots returned to normal conditions, showed a slower restoration of the original form of the head. Two years after the cultures were begun, it was found that the original head form was not displayed by young restored to normal nutrition conditions, the larger helmet being persistent. It seems fairly certain that a new genotype resulted from the long-continued action of the culture medium.[10]

[9] Jennings, H. S., "Heredity and Variation in the Simplest Organisms," AMER. NAT., Vol. 43, No. 510, June, 1909; and other papers by the same author.

[10] "Weitere experimentelle Untersuchungen ueber Artenveranderung speziell ueber das Wesen quantitativer Artenunterschiede bei Daphniden," Sonderabdruck a. d. Verhandl. d. Deut. Zool. Gesell., 1909.

In the experiments of Sumner mice reared in a warm room were found to differ considerably from those reared in a cold room in the mean length of the tail, foot, and ear, and the differences were transmitted to the next generation. The differences may be reasonably designated as being directly individual and somatic, and as having been transmitted by the germ-plasm, which was not subject to the action of various temperatures in the first instance. The reaction forms have an additional claim upon our attention, since they are the ones which distinguish northern and southern races of many animals. The crucial test of the value of the alterations induced in the mice is the one applicable to all of the experimentation on this subject, a test in which two parallel series of cultures, one under the altered environment and the other under usual conditions, should be kept going continuously for a long number of years, lots being withdrawn from both, from time to time, for long-continued comparative culture in normal habitat and under other conditions. Effects due solely to fluctuating variability may be expected to reach a maximum and minimum within two or three years, leaving the enduring effects standing alone, or in such relief as to be capable of ready calibration.[11]

Kammerer carried out some tests with salamanders three years ago which have the interest attached to any attempt to interpret geographic or habitat relations. *Salamandra maculosa* is viviparous when it lives high in the mountains and ovo-viparous at lower levels. *S. atra* is an alpine form and the larvae are large with very long gills. When the latter form was kept at unusually high temperatures the larvæ produced resembled those of *S. maculosa* in its lower warmer habitats. *S. maculosa* kept in low temperatures and without water showed a cumulation of effects by which the characters of the

[11] Sumner, F. B., "An Experimental Study of Somatic Modifications and their Reappearance in the Offspring," *Archiv. f. Entwickelungsmechanik d. Organismen*, Vol. 30, pt. 2, p. 317, 1910.

young and the reproductive habits resembled those of *S. atra*. The conditions of these experiments are not such as to allow a definite separation of somatic and germinal effects, neither was the permanency of the newly acquired habits tested to such an extent as to determine their hereditary value. That characters and habits may be modified in such manner as to appear in the next generation or two in the absence of exciting conditions is illustrated by hundreds of authentic examples in plants which have long been known.[12]

My own earlier work with relation to this subject consisted chiefly of ovarial treatments in which the main and accessory reproductive elements of seed-plants were subjected to the direct action of solutions of various kinds. New combinations of characters constituting a distinct elementary species or genotype were obtained in one plant, and the divergent type has been found to transmit its qualities in the fullest degree as far as tested, to the fifth generation. Still more marked forms were obtained in a second genus, the divergent progeny being lost in transference to the Desert Laboratory, while marked responses have been obtained in the extensions of these experiments upon species representing widely different morphological types in Arizona. The greater majority of the tests have been made upon plants growing under natural conditions, so that environmental reaction in addition to that of the specific reagents might be excluded. Progenies representing many species, including thousands of individuals, many of which are divergent, are now under observation. Absolute finality of decision with respect to the standing of the new types may be reached but slowly.

Gager produced chromosomic aberrations in the reducing divisions of *Œnothera* by irradiations and such excitation was also followed by the appearance of aberrants in the progeny, the hereditary qualities of which have not

[12] *Arch. f. Entwickel.*, Vol. 30, pp. 7–51, 1907.

been tested. Using similar excitation Morgan induced the appearance of white eyes and of short wings in a pedigree culture of the fly, *Drosophila ampelophila*. Both qualities were sex-limited and mendelized when paired with the red eyes and long wings of the original type. Both however seem to be fully transmissible.[13]

A related phase of the subject is that of the interposition of environic factors in mutations and hybridizations. DeVries has repeatedly called attention to the fact that the composition of hybrid progenies of mutants with each other and with the parental form might be altered by nutritive conditions, and the author has cited the fact that mutations were made by *Œnothera Lamarckiana* in the climate of New York which had never been seen in Amsterdam. Furthermore, in discussing the divergent results of DeVries and myself, obtained by crossing the same forms in Amsterdam and New York, the suggestion was made that "the manner in which the various qualities in the two parents are grouped in the progeny might be capable of a wide range of variation. Many indications lead to the suggestion that the dominancy and prevalency, latency and recessivity of any character may be more or less influenced by the conditions attendant upon the hybridization; the operative factors might include individual qualities as well as external conditions."[14]

Using abnormal temperatures for excitation, Kammerer induced color changes in *Lacerta* constituting female dimorphism in one species, and male dimorphism in another, and the newly induced characters, like the original ones, behave in a mendelian manner in crosses, although the heredity has not been carried through enough generations to test their permanence.[15]

[13] Morgan, T. H., The method of inheritance of two sex-limited characters in the same animal, Proc. Soc. for Exper. Biol. and Med., Vol. 8, No. 1, p. 17, 1910.

[14] MacDougal, Vail, Shull and Small, "Mutants and Hybrids of the Œnotheras," Pub. No. 24, p. 57, Carnegie Inst. of Washington, 1905.

[15] Vererbung erzwungener Farbenaenderungen. Arch. f. Entwickl., Vol. 39, Hefte 3 and 4, p. 456, 1910.

Much more striking evidence upon the matter has been recently obtained by Tower in intercrossing *Leptinotarsa decemlineata, L. multitineata, L. oblongata* and other species in their habitats in southern Mexico, and at the desert laboratory. Among other divergences one of the three first generation intermediates characteristic of these cultures was lacking from the Tucson cultures, although two other such forms were included.[16] In a

FIG. 1. Acclimatization shelters and beetle cages, Desert Laboratory (2,600 ft.).

comprehensive treatment of the entire subject with especial reference to modifications in dominance Tower says:

The experiments and observations herein given warrant the general statement that conditions external to a cross are important factors in determining the results thereof. This conclusion has been worked out in both normal and hybrid crosses, in crosses between races which have been created selectively, and between forms which arose as sports;

[16] See Report, Department of Botanical Research, Carnegie Institution of Washington, for 1908 and 1909.

and the second series of experiments in synthesis is sufficient warrant for attributing to this factor a considerable importance in evolution.[17]

Tennent arranged a series of hybridizations of Echinoderms at Tortugas which yielded data of great interest in connection with the earlier conclusions of Vernon, Doncaster, and Herbst as to the influence of temperature and season changes upon dominance. From the information derived from crosses of Hipponoë and Toxopneustes it is clear that the dominance of the parental characters is dependent upon the alkalinity or the concentration of the OH ions. The products of the trial cross fertilization, however, were not reared to maturity.[18]

No phase of the subject under discussion is more readily amenable to experimental investigation, and no results may be expected to bear more directly on the mechanism of inheritance than those in which similar unions give dissimilar progenies under the pressure of unlike environments. It is to be noted that everything of value with regard to the influence of environment upon hybridizations has been secured by the introduction of the geographic or climatic element, that is, the unions leading to divergent results have been made in habitats in which the environic complexes differed not in one, but in many features. Thus the climatic components in southern Mexico reach dissimilar maxima and minima and run unlike courses from those of Arizona.

This method of transplantation of organisms to distant localities furnishing congeries of climatic factors markedly different from those of the habitat in which they were found is one which offers opportunities of the broadest kind, and such exchanges have been made between fresh and salt water, cave and surface, alpine

[17] Tower, W. L., "The Determination of Dominance and the Modification of Behavior in Alternative (Mendelian) Inheritance, by Conditions Surrounding or Incident upon the Germ Cells at Fertilization. (Reprinted from *Biological Bulletin*, Vol. XVIII, No. 6, May, 1910.)

[18] See Report, Director Dept. of Marine Biology, Carnegie Institution of Washington for 1909 and 1910.

summits and lowland plains, high and low latitudes, with results of somewhat limited value until recently. The first of these in which plants were used was made by Nägeli, who carried on observational work on a large number of species in plantations of the botanical garden at Munich, detecting certain obvious alterations which did not appear to offer anything of hereditary value.

The more recent work of Bonnier was directed chiefly toward comparison of the vegetative activity, anatomical modification, and developmental habit of plants exchanged between the mountain and low-land. The care used in attempting to transport soils with the plant was almost wholly without direct application, since the character of the soil is so largely a function of climate that the course of a single season would suffice to change or materially modify any transported soil. Such a precaution might have the sole merit of furnishing the transplanted species with a limited amount of some compound necessary for its growth, but any small amount of soil becomes quickly permeated by solutions from the formations below and contiguous to it. Bonnier's results include much that is suggestive, although no effects were secured which did not disappear within two or three seasons after a plant had been removed from the influence of the exciting agencies or returned to its original habitat.

The first realization of results of importance from cultures widely extended geographically has been obtained in the experiments with Leptinotarsæ by Tower, in which various species of these beetles were studied in their habitats in southern Mexico, in open air and glass houses as far north as Chicago, as far east as the Atlantic and as far west as the Desert Laboratory. Facilities for work upon special problems are now being organized at several places and many contributions to the subject may be expected within the next decade.

The plan for work upon the problems of special interest in connection with the Department of Botanical

Research of the Carnegie Institution of Washington, implies the establishment of experimental cultures in localities which furnish distinct types of climate, or which have characteristic complexes of meteoric factors, as indicated by the vegetation indigenous to them. Secondly, these localities have been chosen with regard to their geographical relations so far as possible, in order that the possible and probable fate of migrating species might be studied. The behavior of plants in these localities is

FIG. 2. Santa Catalina mountains as seen from Desert Laboratory. Experimental plantations shown in figures 3 and 4 are located on this range.

recorded as to anatomical alteration and physiological departure. Having detected some such feature of apparent importance, its reappearance in plants from seeds carried to the original habitat and other locations is followed as one line of evaluation. Contemporaneously, the form is taken into the laboratory and here by analytical experimental tests the effort is made to ascertain to what special agencies the departures are due. Four

main locations furnish the chief facilities for these somewhat extensive experiments, which may be briefly characterized as follows. The domain of the Desert Laboratory has a subtropical arid climate, with one cool moist season, one warm wet season, two intervening dry seasons, the vegetation being chiefly composed of spinose xerophytic shrubs and woody plants, with a large number of the more advanced types of desert plants, which carry an immense water balance, such as the cacti and other succulents. The total rainfall is 12 inches, relative humidity falls as low as 5 per cent. for extended periods and the soil moisture remains below 10 per cent. for weeks, and the altitude is 2,300 feet; maximum temperatures of 112°–114°, minima of about 16° F., with a total exposure below the freezing point of from 12 to 80 hours per annum are encountered.

The xero-montane plantation lies at 5,400 feet on the near-by slopes of the Santa Catalina Mountains at the extreme upper edge of the characteristic desert flora in the oak belt of vegetation with a rainfall of 16 to 18 inches per year, minima a few degrees lower than those of the Desert Laboratory, with such an extension of cold nights as to make temperature a distinct limiting factor; relative humidity is extremely low, soil moisture quite as low as that of the base plantation, and the activity of vegetation of the winter wet season which is such a marked feature of the lower plantation is entirely lacking. The meteoric and other agencies carry a constant stream of seeds from this locality into the region of the laboratory.

The montane plantation lies at an elevation of 8,000 feet in a forest of pine, spruce and aspen, with a climate equivalent to that of northern Michigan, the growing season being about 110 days, the winter being characterized by a heavy snowfall and temperatures as much as 20°–25° below zero Fahrenheit. The spring and autumn are dry, and midsummer has the usual manifestation of heavy thunder-storms, in which the precipitation is

slightly less than the amount in the winter. The yearly total is between 35 and 40 inches. The vegetation is characterized by conifers, grasses and a wide variety of herbaceous and shrubby perennials, very few annuals being found here. The mountain streams carry the seeds of the contiguous elevated slopes and valleys in great profusion to the region of the xero-montane plantations and to the lowlands of the character of those around the Desert Laboratory. These three localities form a connected series in which the behavior of the tested species may be expected to offer phenomena of wide significance and of direct bearing on many phases of geographical distribution and evolutionary advance.

The fourth plantation is at Carmel, California, some 800 miles distant in a straight line from the first three, within a thousand yards of the Pacific Ocean in a forest of Monterey pine, the soil being granitic sand, with organic material or humus in some places, and a heavy cement in others. The climate is characterized by a winter wet season, in which the minima are scarcely below the freezing point and the exposure to such low temperatures is for not more than fifteen or twenty hours per year. A period of heavy continued fogs during two months of the midsummer results in minima of 41° F. in July and August, there being almost no precipitation between March and November. The total precipitation is about 18 inches per annum. The place, therefore, has one rainy season, a dry spring and fall, and a cool midsummer, conditions exceptionally favorable for the survival of species introduced from the localities of the other three plantations of the series. It is obvious that if the data concerning the climatic factors are integrated or summarized and placed in parallel columns a ready means is afforded for detecting the causes which prevent survival or facilitate the development of any form in any locality, and a proper analysis of the same facts may also yield direct suggestions as to the nature of the excitation responsible for any departure on the part of a plant removed from one habitat to another.

The groups of species interchanged among the four different localities include material upon which such analysis may be most readily made. In addition, the introductions are also arranged to simulate certain geographical movements and topographical effects. Species from eastern America and from the lower plantations are taken to the montane and xero-montane plantations to meet conditions similar to those they might encounter in a migration toward alpine or arctic regions. Species from the montane locations and from the eastern states are carried to the desert plantations to have the experience of a southward movement, or that of descending mountain valleys, while all of these localities have furnished forms for establishment in the maritime locality characterized by equable conditions in which species may range widely as to latitude and indefinitely as to longitude. The preliminary exchanges included over a hundred species, mostly biennials and perennials; the survivals amount to less than 80, while perhaps not more than a score of these may be expected to yield results of value or interest.

Our increased insight into the nature of natural groups of organisms has shown the necessity and suggested the means of observing certain distinctions and precautions in this work. Thus it is of the greatest importance that the living material shall be shown to be either simple genotypes or that its phaenotypic nature be apprehended in order that the integration and combination of these forms shall not be mistaken for environic effects. When a lot of plants is taken from one plantation to another, data of the original locality are preserved as the stand of the plant in that place serves as the control. If the plant is multiplied vegetatively in the test, it might reveal a possible complex character of the material in bud-sports, but other divergences might be well ascribed to local effects. On the other hand, if introduced in the form of seeds, the possible complex character of the material would soon become apparent, especially if the generations were followed properly. In the actual management of

the cultures, it is found profitable to re-introduce forms from the original or control lot of various species in order to follow the first stages of their adjustment repeatedly.

The earlier introductions were made in May, 1906, but the establishment of the system was not completed until early in 1909. Some of the species have therefore been observed through the fourth growing season in newly encountered habitats, and as the somatic responses are

FIG. 3. Xero-montane plantation (5,500 ft.), Santa Catalina Mts., Arizona.

immediate or nearly so it may be assumed with some confidence that the alterations observed are those which are to be tested as to their transmissibility. It may be of interest to note briefly some of the more salient alterations with some attention to their geographical significance, reserving the discussion of structural details for a more suitable occasion.

1. Many species of perennials native to regions in eastern America with a temperate summer or growing

season 160–170 days in length, and a winter with extended exposures below the freezing point, endure the climate of the montane plantation with lower minima, shorter growing seasons and more arid dry seasons, all seasonal changes being much more sudden and pronounced than those encountered in their original habitats. *Trillium, Arisæma, Roripa, Sanguisorba, Fragaria* and others offer examples of such survival.

2. Perennials as above survive and thrive in the equable climate of the maritime plantation in which much more equable conditions are found than in the original habitats—*Podophyllum, Sanguisorba, Arisæma, Œnothera, Roripa* and *Fragaria.*

It is to be noted that many species of annuals and perennials are supposed to range from the temperate lowlands of New York to similar montane climates farther south in the Rocky Mountain region, and also to the Pacific coastal belt. Critical examination of material representing the supposed inclusion of the species generally reveals differences denoting elementary species or genotypes which might be grouped together in a Linnean treatment. These relationships offer some most interesting probabilities as to derivation and dissemination which may not be touched upon here.

3. Species from the montane plantation survive and show a luxuriant growth in the maritime plantation with various vegetative modifications, of which *Fragaria, Œnothera, Juglans, Scrophularia, Senecio* and *Dugaldea* offer illustrations.

4. Species from the montane plantation survive and show a development somewhat atypic when carried to the foot of the mountain on which they are indigenous. Examples are *Œnothera, Juglans, Scrophularia* and *Fragaria.*

5. Species from the arid region about the Desert Laboratory survive and show atypic activity in the equable maritime climate. Illustrations are offered by the *Opuntias, Parkinsonia* and *Penstemon.* Species from the

equable maritime location do not survive when taken to any of the other plantations, with the single exception of *Fragaria Californica*, the extremes of temperatures being the evident limiting factor.[19]

By the consideration of the responses of plants in the various climates into which they may be introduced in these experiments, it is possible to determine with some accuracy the limiting factors acting for the exclusion of the form in question. The analysis of the responses to changed environment may be briefly given as follows:

Species from locations with well-marked seasons, in which there is a definite contrast between the warm and dry periods or between dry and rainy seasons, show a lessened tendency to sexual reproduction, and a consequent weakened capacity to form fruits and seeds when taken to locations with equable or monotonous conditions. This is a fact well known to the grower of economic plants, the chief examples being offered by bush and tree fruits disseminated to the southward. Fertilization and the preliminary stages of seed formation may ensue as usual, but the absence of the stimulating effect of changing temperatures usually characterizing the close of a season appears to be followed by a lack of development of the fruit. Examples of this are offered by *Arisæma, Salomona, Sanguisorba, Actæa, Podophyllum, Menispermum, Apios Fragaria* and *Phytolacca.* Exceptions are offered by *Senecio, Œnothera* (some species), *Potentilla, Geum* and others.

The transplantation of a species from one type of climatic complex to another generally alters the shoot-habit, or pattern of development of buds. The maritime location is characterized by a profuse development of runners and offsets, and the growth of branches on the lower part of main axis, above or below ground. In some species, the main axis remains in a very rudimentary condition. Excellent illustrations are furnished by *Œnothera, Scrophularia, Dugaldea* and *Phytolacca.*

[19] See Kuckuck, P., "Ueber die Eingewöhnung von Pflanzen wärmerer Zonen auf Helgoland," *Bot. Ztg.*, Vol. 68: 49–86, April, 1910.

The removal of the higher types of plants from the desert conditions with which they articulate, that is, extreme forms with reduced shoots and swollen stems, is followed by increased development of spines when grown

FIG. 4. Montane plantation (8,000 ft.), Santa Catalina Mts., Arizona.

under equable conditions, or in climates with greater water supply as illustrated by *Opuntia santa rita* and other "spineless" forms.

The removal of plants from localities with well-marked seasons to equable maritime climates is followed by a leaf development which may result in the multiplication of the parts. *Fragaria.* All introductions in which the range of climatic conditions to which the plant was subject was narrowed, were followed by increased vegetative activity, which multiplied underground branches and propagative bodies.

The concurrence of these responses in a single form may be well demonstrated by the results of studies of a genotype near *Scrophularia leporella,* found in the vicinity of the montane plantation, which has survived in the shade at the Desert Laboratory and at the seaside locality. In its native habitat, it shows a strict, scarcely branching shoot with a few fleshy succulent roots, which apparently carry water with a small dissolved content. When this form is taken to the Desert Laboratory, its reproductive season is lengthened from two months to five or six months, although but few seeds are formed, the shoots branch more profusely, and a greater mass of underground members are formed. In the maritime location these features are accentuated and the development of branches goes on to such extent that the shoot gives rise to a number of main branches which can not be supplied with water, and hence soon wilt and die. The underground system now includes dozens of thickened members from one to two centimeters in diameter, which may show a total weight of from 6 to 8 kilograms.

The removals of forms included in the experimental series may be taken as fairly parallel to the distributional movements effected by various agencies without the intervention of man. Some, as a matter of fact, are exact duplicates of occurrences in which these same species participate. The alterations noted are undoubtedly environic effects, and may be attributed chiefly to climatic factors. Two common assumptions as to the behavior of plants are to be noted when species are removed to localities widely separated from the habitat in which they are

found. If they fail to survive or do not flourish in the second location, they are said to have failed to adapt themselves to the new conditions. Into this statement may be read one more in accordance with a physiological consideration of the matter to the effect that the intensities of some of the factors present exceeded the maxima of the plants in question and thus acted as limiting factors to their proper or full development or survival.

The second assumption is to the effect that the alterations displayed by a plant in newly encountered habitats are adaptive and that these changes render the organism displaying them better fitted to meet the conditions. Some reactions are of such a nature as to be of benefit to the plant displaying them, but the worker who assumes that this is true of all changes even in species which thrive and luxuriate in the new habitats will soon find himself widely afield from facts capable of being substantiated by experiments. Thus in the case of the *Scrophularia* noted above, the new maritime habitat includes a congerie of agencies which incite it to form enormous clusters of thickened roots and to exhibit the habit of branching densely. So many branches are formed in fact that the conducting channels at the base of the shoot are incapable of carrying a supply of water adequate to the transpiratory needs of the foliar organs, although the vastly increased balance in the root-system would be sufficient to meet the needs of the plant for days, and consequently the widely spreading shoots of these plants show a large proportion of branches which have about reached maturity and are dying. The behavior of the semi-spineless opuntia (*O. santa rita*) offers illustration of the same sort. Bearing only a few or no spines in its native mountains, the new segments in the cool foggy climate of Carmel are spinose at almost every areole. Here the result is very plainly one of the awakening of a latency, since it seems fairly clear that this plant and all of its relatives show spines as a final stage in the reduction of the shoot system, and that the spineless form is the culmination of a line of progress. The

reappearance of the spines is, therefore, one of regression; in a paper before this society a year ago I was able to present results of experimental parasitism, in which the reactions of autophytic green plants when grown as parasites included a number of phenomena, which were not only not adaptive in any sense, but which might reasonably be considered as distinctly unsuitable. Among these was included the very striking autonomic movements of etiolated segments of the prickly pear (*Opuntia*) when it was led to fasten upon other plants as a parasite.[20]

Many alterations in plants in the cultures, however, particularly those concerning the reproductive habits, may readily be interpreted as being adjustments of a directly adaptive character. With these are many correlative changes which are simply carried along. It seems fairly certain that the distinction between the primary adjustive alterations and correlative effects will be made clearer in any analyses made of the possibilities of inheritance of somatic changes. In connection with the discussion of the nature of the parasitic adjustments the behavior of a drop of water when resting upon a rough surface was offered as an illustration of the modifications of an organism under environmental influences. The sectors of the drop in direct contact with a hard object which is not wetted will be most markedly and directly altered, in a manner parallel to the reactions in functions most directly affected by environment, while the free sectors or qualities of the drop or of the organism will be altered in various degrees by correlation stresses.

So far as the responses in the cultures at the four plantations are concerned, they appear to the fullest extent at once and in the first generation. Whether any of them may become fixed and transmissible in a long series of generations subjected to the same conditions, like *Daphnia*, remains to be determined. That this might be the most

[20] MacDougal and Cannon, "The Conditions of Parasitism in Plants," Pub. No. 29, Carnegie Institution of Washington, 1910, p. 37.

important feature of all experiments of this kind was pointed out three years ago.[21] Although our attention has been focused chiefly on the possibilities of the transmission of somatic effects by seed reproduction, yet it is to be recalled that the continuation of an alteration by fissions, division or cuttings might come to have great biological significance.

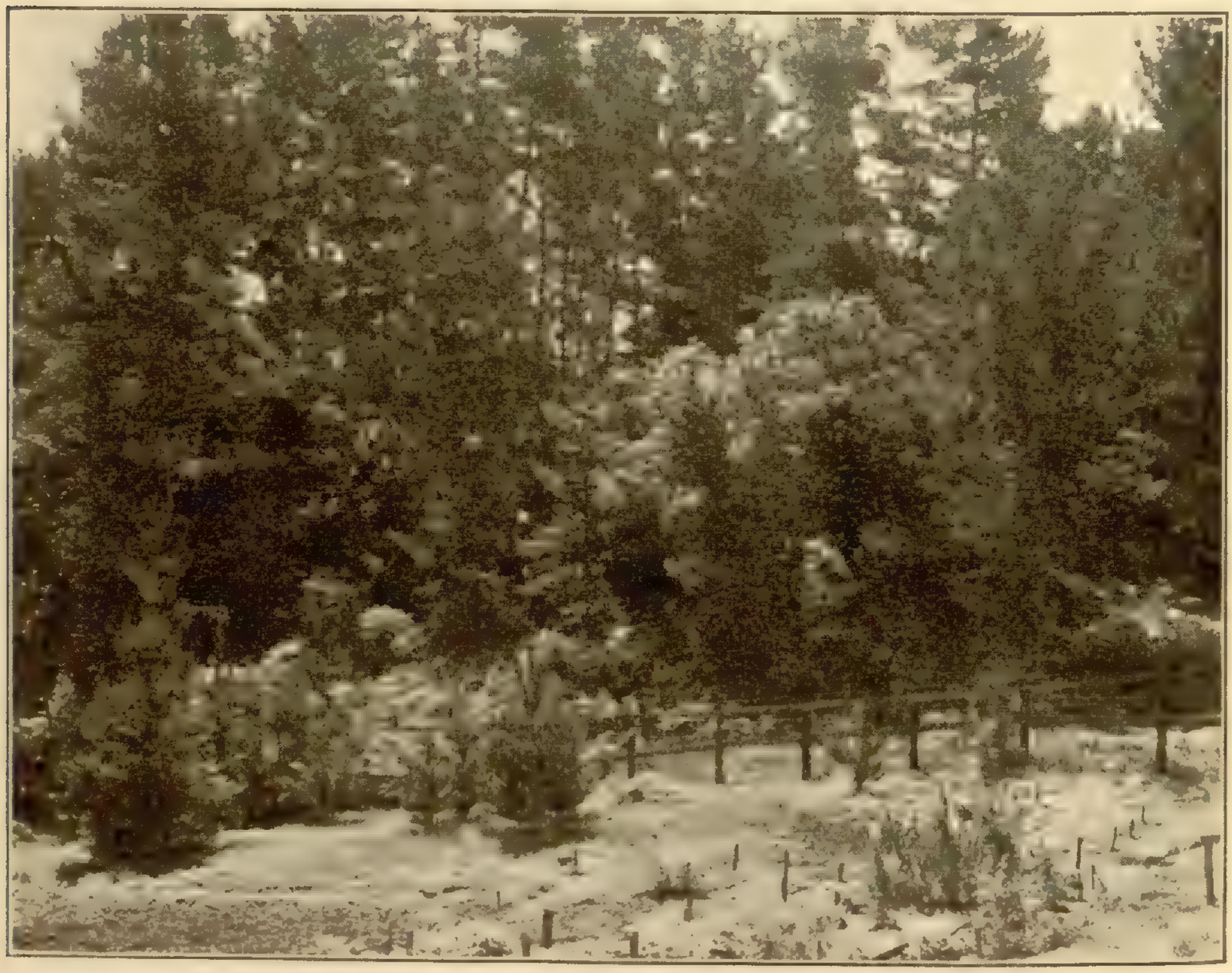

FIG. 5. Maritime plantation near the sea-shore, Carurel, California.

Jennings would consider the *Paramœcia* as free germ cells subject to the direct action of environment, and themselves propagating by simple division if his meaning is properly apprehended. If this is allowable, the same conception may be extended to include cuttings and all fission methods of reproduction in plants, even of the most advanced types. As a general rule, when a portion of the sporophyte of a plant, such as an offset, runner, stolon, tuber, bulb, corm or other detached branch produces a new individual, the mature characters of the parent disappear in the regeneration or sprouting and the

[21] "Fifty Years of Darwinism," 1909.

ontogenetic procedure of the plantlet will be much like that of a seedling.

The exact observation of the manner in which environic effects may pass the regeneration stage and reappear has not yet been made to any great extent. Doubtless many conditions will be found to affect the process. Bud sports, or vegetative mutations, are, of course, fully transmissible along a series of stages of division by cuttings, and many of them have been found to transmit their divergent characters by seed resulting from close pollination. Mechanically considered, the vegetative reproduction of a plant consists simply of its perpetuation through an unbroken chain of metameres or internodes, each joint arising from a growing point borne terminally or laterally by its predecessor. The projection of induced characters formed by metamere *A* into metamere *B*, therefore, involves the question of germplasm as represented by the embryonic mass of the growing points with no opportunity for carrying over structures mechanically as in the *Paramœcium*. The comparative action in heredity when plants are transported to new climates through bulbs and tubers and through seeds is one that has not yet been made, although doubtless horticultural and agricultural literature is rich in the records of facts upon which decisive generalizations might be made.

The genetic character of environic effects remains to be considered. In any species or genotype there is, withal, a limited number of things included within the morphological possibilities. The appearance of any character in an acclimatization culture raises a question at once as to the standing of the new feature. Is it a regressive character, once displayed by the species and now recalled by the very conditions under which it was first induced, or is it to be considered as a character *de novo*, arising simply and directly in response to the external agencies which have been seen to induce it? Thus in the results cited above, our general knowledge of the Cactaceæ leads us to assert with some confidence that the reappearance of a full complement of spines in a prickly

pear from which they had all but disappeared is a regression or return to the condition of the greater majority of the group, a condition which must have been shared by its ancestors at no remote stage in its progressive development.

None of the attempts hitherto made to perfect a theoretical conception which would be useful in interpreting the mechanism of environic responses have had anything more than the most limited usefulness. The stimuli of climatic and many other agencies do not imply the introduction of any strange or new substances into the bodies of the organs affected. These agencies might change the dissociations in such a manner as to modify the relative number of free ions and thus alter the molecular complex of the living matter in a very important manner. The intricate play of enzymatic action might also be altered, and any modification of the relative reaction velocities of the more important processes might result in material and permanent change, especially in those cases in which external agencies interfere directly with the action of the germ-plasm.

The introduction of solutions into ovaries or the exposure of reproductive elements to unusual irradiation may raise the additional liability of disturbed polarity and of modified surface tensions in the cells. It is conceivable that the rearrangement or disturbance of the localizations of substances, especially the mineral salts, might seriously modify the capacities of the bearers of heredity. These direct and material possibilities offer an adequate basis for the organization of experimental research upon the main subject, as well as the means of interpretation of results without recourse to schemes of particulate inheritance or theories as to the constitution of germplasm to which may be ascribed usefulness in the discussion of other problems in evolution.

The theoretical consideration of the subject which seeks to assign all cases of inheritance of environic effects to the direct action of the existing agency upon the germplasm in itself is one to be regarded with some wariness, as it may lead us into empiric assumptions which may

conceal rather than visualize the actual occurrences. Direct germinal effects are undoubtedly secured in ovarial treatments, and Tower's analytical cultures showed that certain somatic characters induced directly might be secured also by direct excitation of the egg. Such concurrence of reaction may be expected especially with regard to some qualities of simpler organization. Not so readily interpreted are the responses of *Sempervivum*. Alterations in size, number, and structure of floral organs brought about by excitation during ontogeny are surely not coordinate with changes in the germ plasm induced simultaneously. In the case of *Capsella* the transference to an alpine habitat of the plant in the shape of seeds is followed by immediate and direct ontogenetic alterations affecting a multitude of characters. Not until these somatic responses have been repeated, dozens, scores, or perhaps hundreds of times, is an impression made on the germ-plasm that allows it to carry the new characters in the absence of the inducing. These facts suggest to us that the soma is in the closest association with the germplasm, has both theoretical and actual qualities different from it, and any changes in these must inevitably be communicated, by the action of hormones or other physiological mechanisms.

A brief paraphrase of the foregoing discussion may be useful in emphasizing some of the more important matters which have been touched upon. It is readily apparent that the assumption of the inheritance of acquired characters, after a long period of tolerance, with but little research activity bearing upon its principal claims, is coming in for a large share of attention from the experimentalist, and there seems a fair prospect that decisive facts may be obtained within a period, very brief in comparison with the century since the principal tenets of the theory were first formulated. Already results are available which have been obtained by cultures of animals from paramoecia to mammals, and of plants from bacteria to the higher seed-plants.

A critical consideration of the available information seems to justify the following generalizations:

External agencies acting upon bacteria, crustaceans, beetles, fungi, and some of the higher types of seed plants have been seen to result in the appearance of new types or genotypes, which have been found to transmit their characters perfectly through so many generations as to indicate practical permanency.

In the greater majority of such cases of changes in heredity, inclusive of Tower's cultures of beetles, Woltereck's experiments with *Daphnia,* Morgan's results with flies, and my own ovarial treatments of seed plants the germ-plasm was exposed to the excitation of unusual climatic factors, irradiation, concentrated nutritive media, or of solutions of sugar or inorganic salts.

The new qualities were seen to be fully displayed, and to appear in a mutational manner in all of these instances, although the new head form acquired by *Daphnia* in Woltereck's experiments did not become fixed and fully heritable until the organism had been kept under the influence of the exciting agency for an extended period, nearly two years. The most recent and one of the most interesting series of results are those which show that the influence of environic factors upon hybridizations by excitation of the germ-plasm may alter materially the results of the unions of identical pairs. This seems to have been first suggested by De Vries and to have been seen by MacDougal in hybrids of mutants of *Œnothera,* while it has been established beyond doubt by the extensive and conclusive results of Tower in crossing beetles under various conditions that environic agencies may exert a very marked effect upon the dominancy of paired characters and the general composition of hybrid progenies. A different phase of the matter is represented by the experiments of Kammerer, in which, characters constituting temporary sexual dimorphism mendelize when paired. Aberrants, sports or mutants have been seen to arise and perpetuate themselves under unusual culture conditions in yeasts and bacteria, their survival being dependent upon pedigreed cultures in some cases; and the successive generations were those resulting from fissions, although in some cases spores were interposed.

Many of the purely accommodative adjustments displayed by these organisms and by *Paramœcia* as well as the extremes of variability induced by external agencies and continued by selection, do not become fixed and are not transmissible even in a series of generations by fission. The recent work of Pringsheim, however, shows that some alterations in the way of accommodations or functional responses of yeasts and bacteria to unusual temperatures, culture media, and toxic substances become fixed and transmissible both by fission and through spores. It is not clear, however, that the differential action of the exciting agent upon soma and germ can be made out, and perhaps nothing more definite might be said than that both are directly and simultaneously exposed and exhibit coincident reaction.

When we pass to a consideration of the results of Zederbauer and Klebs, however, the evidence becomes much more decisive. A *Capsella* was found growing at an elevation of 2,000 to 2,400 meters in Asia Minor which had hairy stems, 2–4 cm. long xerophytic leaves, and reddish flowers. This plant had been evidently introduced from the lowlands by man along a route that has been in use for more than 2,000 years. The *Capsella* of the lower plains forms a stem 30–40 cm. high, has whitish flowers and broad leaves; when its seeds are taken to elevations with climates comparable to the above, individuals are developed duplicating those of the highlands, so that the characteristic features of this alpine form are clearly direct somatic reactions; and that they have become fixed and fully transmissible is demonstrated by the fact that in a series of generations grown at lower levels the stem characters, as well as those of the reproductive branches and floral organs, retained their alpine acquired characters, although the leaves, as might be expected, returned to a mesophytic form with broad laminæ.

The results obtained by Klebs include divergences of stem habit, number and structure of floral organs in *Sempervivum* which are not capable of being interpreted as functional or adaptive responses to the agencies which called them out and were found to be fully transmissible

by seeds, in which case it is fairly clear that somatically produced characters have been impressed upon the germplasm and carried by it to succeeding generations. The structural and functional features displayed by *Sempervivum* in these laboratory experiments are not adaptive in any sense in contrast with those of *Capsella,* which are direct responses.

The actual transplantation of organisms from one locality to another, as a method of experimentation, promises the results of highest value and widest significance, especially when taken in connection with analytical laboratory cultures. This method of approach is one which may yield evidence of the greatest value upon the influence of isolation and other geographical factors, but is also one which allows the repetitive or mnemonic effects to be evaluated. When supplemented by laboratory analyses and cultures to determine the nature of alterations induced, such methods promise results of the greatest value. A series of plantations including locations from mountain tops to the seashore has been established in connection with the Desert Laboratory in accordance with this idea, and in addition to the interchange of species from the various localities a number of introductions have been made from eastern America. Negative or positive results of sufficient inclusiveness to permit analyses as to the nature of the exciting agency and the permanence of the response are yet available.

Some of the characters called out by environic agencies may be retracements, or regressions, as the reappearance of spines in cacti, or they may be awakened latencies or organizations *de novo.* Some of the responses may result in sexual dimorphism, while in others the induced characters may be sex-limited. The alterations induced by external agencies may be cumulative or mutative as to appearance or organization, and they may be permanent upon first appearance, or on the other hand may need generations of repetition before becoming fixed. And lastly the changes may be orthogenetic or heterogenetic as to direction, adaptive and accommodative or correlative, or wholly inutile as to their functional relations.

THE NATURE OF GRAFT-HYBRIDS

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THE possibility of hybrids arising as the result of grafting long has been a mooted point and the subject has given rise to much discussion.

The history of the small number of graft-hybrids that have hitherto been recorded is small and is not as complete as might be wished; indeed it has been claimed repeatedly that these supposed graft-hybrids are not really such but have been produced by the ordinary method of cross-fertilization. The most famous of these graft-hybrids is the much discussed *Cytisus Adami* which originated at Vitry near Paris about 1826. This was said to have been the result of grafting *Cytisus purpureus* upon *C. laburnum*. A series of supposed graft-hybrids is also recorded resulting from grafts between a thorn, *Crataegus monogyna*, and the medlar, *Mespilus germanicus*. Three of these graft-hybrids were secured by Bronvaux. The hybrids in this case were not all alike and were given special names and the genus *Cratægo-mespilus* was proposed for these bi-generic hybrids.

Of the recent opponents of the graft-hybrid theory the best known is the distinguished botanist Professor E. Strasburger, of Bonn. Strasburger made a careful cytological study of *Cytisus Adami* which has been retained in cultivation ever since its origin some eighty-five years ago. Strasburger came to the conclusion that *Cytisus Adami* was a real sexual hybrid and not a graft hybrid. He believes that if the latter were true the nuclei of the hybrid would show a double number of chromosomes. This, of course, implies that in hybrids arising otherwise than sexually, assuming that a nuclear fusion would precede the formation of such a hybrid, there would be no

reduction division of the nuclei comparable to that which normally occurs before the fusion of the sexual cells in normal fertilization.

FIG. 1. *A*, seedling of the black nightshade, *Solanum nigrum*; *B*, seedling of a tomato, *S. lycopersicum*; *C*, shoot of the graft-hybrid, *S. tubingense*; *D*, *E*, leaves of the graft-hybrid, *S. proteus*. (All figures after Winkler.)

Němec,[1] however, believes that a reduction division does occur, and there is, therefore, no reason to expect

[1] Němec, B., "Zur Mikrochemie der Chromosomen," *Ber. der deutsch. Botan. Gesellsch.*, 27, 46, 1909.

an increase in the number of chromosomes in the cells of the hybrid. If such a reduction does occur *Cytisus Adami* would show the same number of chromosomes as *C. laburnum* which has the same number as *C. purpureus.*

The study of graft-hybrids has assumed a new interest through the very important recent investigations of Professor H. Winkler, of Tübingen. These investigations prove beyond question that graft hybrids are possible, and the numerous experiments carried out with every possible precaution and showing remarkable ingenuity as well, furnish by far the most important study on the nature and origin of graft-hybrids that has yet been published. These experiments are being further developed by Professor Winkler but the results already obtained are of the greatest interest and value.[2]

The fact that hybrids may arise as a result of grafting touches some of the fundamental problems of heredity, and this makes these papers of Professor Winkler of the highest importance to all students of heredity, and they deserve much wider attention than they have as yet received.

The plants chosen by Winkler for his experiments were the black nightshade, *Solanum nigrum*, and two varieties of the tomato, *Solanum lycopersicum*. These two species are very distinct, and indeed many botanists regard the tomato as belonging to a distinct genus *Lycopersicum*, so that Winkler's graft-hybrids might be regarded as bigeneric like the *Cratægo-mespilus* graft-hybrids.

The methods by which Winkler secured his graft-hybrids were extremely ingenious. Seedlings of the night-

[2] 1. "Uber Propfbastarde und pflanzliche Chimæren," *Ber. d. deutsch. botan. Gesellsch.*, 25, 568–576, 1907.

2. "Solanum tubingense, ein echter Propfbastard zwischen Tomate und Nachtschatten," *ibid.*, 27, 595–608, 1908.

3. "Weitere Untersuchungen über Propfbastarde," *Zeitschr. für Botanik*, 1, 315–345, 1909.

4. "Uber die Nachkommenschaft der Solanum-Propfbastarde und die Chromosomenzahlen ihrer Keimzellen," *ibid.*, 2, 1–38, 1909.

5. "Uber das Wesen der Propfbastarde (Vorläufige Mittheilung)." *Ber. der deutsch. botan. Gesellsch.*, 28, 116–118, 1910.

shade and of the tomato were decapitated and reciprocal grafts were made. In making these unions the graft was cut either wedge-shaped or saddle-shaped at the point of junction with the stock. The graft and stock united readily whether the nightshade or tomato was used as the stock. After the union was complete the plant was again decapitated, the cut being made through the region where the union had taken place. The cut surface thus exposed is composed of tissue derived from the two members of the union and from this cut surface a callus soon develops from which numerous adventitious buds quickly arise. It was thought that from some of these adventitious buds arising at the point of the junction of the graft and stock there might be produced shoots which would combine the characteristics of the two, or at least might be composed of tissue derived from the two parents.

Naturally the great majority of the shoots arising from the cut surface of the stem were either pure nightshade or pure tomato. But finally shoots were observed which were evidently of mixed origin. The first of these graft-hybrids were obviously composed of pure elements derived from the two parents. Some of these shoots were almost equally divided by a median line on one side of which the organs—stem, leaf, etc.—were those of the nightshade, while on the other the organs were evidently derived from the tomato. Sometimes a leaf was nearly equally divided. In most cases one or the other of the parents predominated, but there was no intermediate region between the two kinds of tissues and organs. It is clear that such monstrous forms, for which Winkler proposes the name "chimæra," are not hybrids in any true sense of the word, but have arisen from buds in which there was a mere mechanical coalescence of tissue from the two parent forms at the junction of the stock and graft.

Further experiments, however, resulted in the production of shoots in which the characteristics of the two parents were so intimately combined, that their discov-

erer felt warranted in assuming that these were really hybrids, probably arising from the actual fusion of cells derived respectively from the nightshade and the tomato, this fusion taking place where the graft had united with the stock. This cell-fusion was assumed to involve a fusion of the nuclei as well, analogous to the fusion of the egg-nucleus with the generative nucleus of the pollen tube in normal fertilization.

Several types of these graft-hybrids were produced and to these specific names were given.

The first genuine graft-hybrid was called *Solanum tubingense* and it has since been produced several times and has been propagated by cuttings and distributed to various botanical gardens. During the past summer I had an opportunity of seeing this graft-hybrid growing well in the botanical gardens of the University of Munich.

Solanum tubingense is intermediate in external appearance between the nightshade and tomato but is rather nearer the former (see Fig. 1, *C*). The nightshade (*A*) has simple, smooth-edged, oval leaves and an almost smooth stem. The tomato (*B*) has compound leaves with sharply serrate leaflets and all of the varieties are strongly hairy. The hybrid (see Fig. 1, *C*) has simple leaves but they are sharply serrate or often slightly lobed like the leaflets of the tomato, and both stem and leaves are abundantly provided with hairs.

The flower in *Solanum tubingense* is also intermediate in character. The nightshade has small white flowers with a smooth calyx whose lobes are very short. The flower of the tomato is much larger, bright yellow in color and the lobes of the calyx are hairy and very much longer than those in the nightshade. The hybrid has flowers which are intermediate in character. They are larger than those of the nightshade but much smaller than those of the tomato, but like the latter the flowers are a pronounced yellow. The calyx lobes are two or three times as long as those of the nightshade but much shorter than those of the tomato. Like the latter, how-

ever, there are numerous hairs upon the calyx lobes which in the nightshade are almost smooth.

The fruit of *Solanum tubingense* is very much like that of the nightshade but is rather larger, and although it is black in color there are some traces of the red or yellow color of the tomato.

Four other well-marked graft-hybrids were secured to which were given the names *Solanum proteus*, *Solanum darwinianum*, *Solanum koelreuterianum* and *Solanum gaertnerianum*.

The first of these originated in a most peculiar fashion. A chimæra was obtained which consisted of *two* hybrid components. One of these was the before mentioned *S. tubingense* while the other was a hybrid which was more like the tomato. This chimæra soon divided into two branches one of which was pure *S. tubingense* and the other the new hybrid, *S. proteus*. The latter was then removed and rooted and further propagated by cuttings. This species has very variable leaves (see Fig. 1, *D*, *E*) which on the whole are more divided than those of *S. tubingense*, while in the characters of the flower and the fruit it is more like the tomato than like the nightshade.

Both of the forms *S. koelreuterianum* and *S. gaertnerianum* were produced more than once and they are respectively more like the tomato and nightshade but each differs in important particulars from either of the parents.

The form, however, which is of the greatest interest is the hybrid to which Winkler gave the name *S. darwinianum*, the third to result from his experiments. This hybrid arose in a quite different manner from the others and great ingenuity was shown in isolating and propagating it. The shoot from which this hybrid originated was a chimæra which developed from a graft of a tomato upon a nightshade. This chimæra was made up principally of pure *Solanum nigrum*, but a small portion of it consisted of tissue which was different from any

of the forms which had yet been discovered. The chimæra instead of being made up of two portions united longitudinally was composed mainly of tissue evidently of pure *Solanum nigrum* origin. A small strip, however, near its base was of a different character. This region consisted of a single leaf, and a small amount of tissue lying below belonging to the stem. The same form was secured a second time where it developed from a five-fold chimæra derived from *S. proteus*. Unfortunately, it was not possible to propagate this second specimen.

In order to isolate this new form it was necessary to cause the axillary bud belonging to the single leaf to develop into a shoot. This was finally successful after four decapitations of the *Solanum nigrum* shoot above it. The final result was a branch which was very different from any of the previously developed forms and it was named *Solanum darwinianum*. The point of special interest in connection with this form is that of all graft-hybrids which Winkler secured, this seems to be the only one which is likely to prove a hybrid in the strict sense of the word. This point, however, will be brought out later in the discussion of the real nature of these graft-hybrids.

All of the hybrids were propagated further by cuttings and with the single exception of *Solanum koelreuterianum*, were made to produce ripe fruit which in all cases was more or less intermediate in character between the fruit of the nightshade and the tomato. In *Solanum darwinianum*, however, the fruit was all sterile and no perfect seeds were formed. The fruit itself is a small round berry like the fruit of the nightshade in form, but having the color and structure of the tomato. In *Solanum koelreuterianum* the young fruit set but failed to reach maturity.

Of the hybrids *Solanum tubingense* is the most fertile and produces fruit very abundantly. A considerable number of the fruits, however, are sterile or "parthenocarpic" and the seeds in no cases reach their full de-

velopment. Nevertheless Winkler was able to make these seeds germinate and the second generation of the plants was reared. *S. gaertnerianum* produces fruit only in small numbers but the seeds are perfectly developed and germinate readily, the same being true of *S. proteus*.

REVERSIONS

Winkler observed a number of cases where the graft-hybrid reverted to one or other of the parent forms. Similar cases of reversions have been recorded for *Cytisus Adami* and *Cratægo-mespilus*. These reversions were studied with special care in his first hybrid *S. tubingense*. In several instances where the plant was cut off below the first lateral bud numerous adventitious shoots arose from the cut surface, and while some of these were pure *S. tubingense*, others were pure *Solanum nigrum*, the parent species which is nearer to *S. tubingense*. In a similar manner *S. proteus* was observed frequently to revert to the tomato, but in no case was there reversion to the nightshade.

Sometimes spontaneous reversions occur. Thus in *S. tubingense* the apex of a plant was noted which had suddenly assumed the characters of *S. nigrum*. Winkler gives an excellent photograph of this plant. In other cases shoots of mixed nature were seen, some having the structure of chimæras, half nightshade and half the hybrid form. In these mixed shoots the inflorescence had flowers of two sorts belonging respectively to the nightshade and to the hybrid. Similar mixed inflorescences have also been observed in *Cytisus Adami*.

The Second Generation

In *S. proteus* and *S. gaertnerianum* perfect seed is developed and germinates readily. *S. tubingense* which sets fruit freely never has the seed fully developed but as we have already stated Winkler succeeded in germinating these seeds and rearing plants from them. He

explains the failure of the seeds to develop fully to the fact that the fruit of the hybrid, which closely resembles that of the nightshade, ripens before the seeds have had time to complete their development. The tomato fruit requires a very much longer time for maturing than does the berry of the nightshade and a correspondingly longer time is needed for the seed to be perfected; and he thinks that the longer time required for the seed development in *S. tubingense* is an inheritance from the tomato parent, while the fruit is mainly of nightshade derivation.

All of the seedlings derived from these hybrids reverted absolutely to that parent form which the hybrid more nearly resembles. Thus the seedlings of *S. tubingense* and *S. gaertnerianum* are pure *S. nigrum*, those of *S. proteus* pure tomato. This behavior also corresponds to that of the very few cases where seedlings have been secured from *Cytisus Adami*, these in all cases proving to be pure *Cytisus laburnum*.

Of the *Cratægus-mespilus* hybrids only one, *Cratægomespilus asnièresi* produced seed capable of germinating. These seedlings were not reared to maturity but so far as could be judged from the young plants, were pure *Cratægus monogyna*, the parent which the hybrid more nearly resembled.[3]

The third and fourth generations of the *S. tubingense* seedlings retain perfectly the characters of *S. nigrum* and the same is the case when they are cross-pollinated by *S. nigrum*. Attempts to cross *S. tubingense* with the tomato resulted in the formation of fruit but no seeds were developed. It may be also recorded that crosses between the two parent forms, the nightshade and the tomato, were without any result.

S. proteus crossed with the two parent forms produced seed when crossed with the tomato to which it stands the nearer, and sterile fruit when crossed with *S. nigrum*.

[3] Noll, F., "Die Propfbastarde von Bronvaux," *Sitzungsber. der niederrheinische Gesellsch. für Natur- und Heilkunde*, 1905.

As yet no seed has been obtained from crosses between the graft-hybrids themselves.

The Nature of Graft-Hybrids

Winkler concluded at first that all the graft hybrids except the chimæras probably arose from actual cell fusion and might be compared directly with hybrids arising from true fertilizations. It was suggested by another student of graft-hybrids, Bauer,[4] that these apparent true hybrids might also be chimæras of a type which he has called "periclinal," *i. e.*, the outer tissues are derived from one parent, and the inner tissues from the other, but none of the tissues themselves are of hybrid nature. This hypothesis seemed the more probable from the results of investigations of MacFarlane upon *Cytisus Adami*[5] in which he showed that the epidermal tissues were strikingly like those of *C. purpureus* while the inner tissues were like those of *C. laburnum*. An investigation of the *Cratægo-mespilus* hybrids revealed a similar state of affairs.

Acting on this suggestion Winkler made a careful cytological study of his hybrids and found that four of them were indeed periclinal chimæras. But one of them seemed to be a real hybrid resulting apparently from a fusion of cells at the junction of the graft and stock.

The nuclei in the nightshade and the tomato differ very much in the number of the chromosomes so that the determination of the origin of the tissues in the hybrid is made comparatively easy. The chromosome number in the sporophytic tissue is twenty-four in the tomato and seventy-two in the nightshade. These numbers were found in the tissues of all of the graft hybrids except *S. darwinianum* where the reduced number of the

[4] Bauer, Erwin, "Propfbastarde," *Biologisches Centralblatt*, 33, No. 15, 497–514, 1910.

[5] MacFarlane, J. M., "A Comparison of the Minute Structures of Plant Hybrids with those of their Parents, and its Bearing on Biological Problems," *Trans. Roy. Soc. of Edinburgh*, 37, 203–286, 1895.

chromosomes in the germ cells was found to be twenty-four, which was to be expected if these were derived from cells with forty-eight chromosomes; *i. e.*, one-half the number of the twenty-four plus seventy-two chromosomes of the two parents. It is assumed by Winkler that a reduction in the number of chromosomes follows the fusion of the cells. He says:

> This chromosome number, *i. e.*, forty-eight, is most readily explained by the assumption that in the formation of the graft hybrid a nightshade cell (with seventy-two chromosomes in its nucleus) and a tomato cell (with twenty-four chromosomes) united. The resulting cell, from which the subepidermal layer at the apex of the darwinianum hybrid arose, had a nucleus with ninety-six chromosomes which then underwent a reduction division resulting in forty-eight chromosomes.

This study of the tissues of *S. darwinianum* indicates that the subepidermal tissue from which the sporogenous cells develop is of genuine hybrid nature arising from a fusion of cells including the nuclei derived from the two parent forms.

In his latest paper (5) Winkler gives a brief summary of his conclusions which are as follows:

> Hybrids may be arranged in two groups, sexual and graft hybrids. The latter may be divided into three classes according to the theoretical possibility of their method of origin, viz.: (1) Fusion graft-hybrids arising from a fusion of two somatic cells derived from distinct species. (2) "Influenced" ("Beeinflussungs Propfbastarde") graft-hybrids which arise from specific influences of one graft component upon the other without cell fusion (as through chemical substances, translocation of cytoplasm, etc.). (3) Chimæras, in which specifically pure cells from both graft components are combined to form a new individual. These chimæras may be: (*a*) Sectorial chimæras in which the two sorts of cells in the growing point are divided by a longitudinal plane. (*b*) Periclinal chimæras in which the periclinal cell layers of the growing point are furnished respectively from one or the other parent form. (*c*) Hyperchimæras in which the growing point is made up of a mosaic of cells derived from the two parent forms.

The first of Winkler's graft-hybrids were unmistakably chimæras of the first type. Of his later graft-hybrids to which he gave special names, all except *S.*

darwinianum are periclinal chimæras. This is true also of *Cytisus Adami* and the *Cratægo-mespilus* hybrids. Thus *S. tubingense* has its epidermal region derived from the tomato while the inner tissues including those which give rise to the sporogenous cells are of nightshade origin. In *S. proteus* the reverse is the case. This explains all cases of reversion to the parent forms and also the character of the seedlings which in the one case are pure nightshade and in the other tomato, this being due to the fact that the spores (pollen spores and embryo-sacs) arise from sub-epidermal tissues derived from the nightshade or the tomato as the case may be.

These remarkable experiments of Winkler's must be of the greatest interest to all students of the problems of heredity. They emphasize a fact, too often overlooked, that it is not always safe to apply to the study of plants the data of zoology. It must be remembered that in the evolution of the higher plants there has been a constant tendency toward a reduction of the sexual reproductive parts. Many biologists quite ignore the fact that the flowering plant, as it is generally understood, is a purely sexless organism. The so-called sex organs, stamens and carpels, are not such at all, but are non-sexual sporophylls.

The sexual generation of the highest seed plant is a far simpler organism than that of the moss or fern and the sex organs are correspondingly simpler. Moreover the development of the sex cells and the extraordinary correspondences in nuclear structure, the reduction divisions and the mechanics of fertilization must have developed quite independently of these phenomena in animal cells, since the two great divisions of organisms, plants and animals, parted company for good long before the elaborate structures found in the higher members of the two series were developed. Hence it by no means follows that what is true in one case must necessarily follow in the other.

With the subordination of the sexual generation of

the higher plants there goes a high degree of regenerative power, a great contrast to the very limited capacity for regeneration shown by the highly organized animals where new individuals can only arise through sexual reproduction. This great power of regeneration in plants is accompanied by much less specialized cells and a very imperfectly marked individuality of the organism as a whole. Any seed plant may be regarded as a colony of individuals since the parts are repeated indefinitely and can be made to regenerate the whole plant. The power of regeneration shown by almost any part of the plant, even a single cell in some cases, renders any theory of a special germ plasm out of the question in the case of plants, however plausible such a theory may appear when applied to animals.

It is not then so very extraordinary that this regeneration of the plant from somatic cells should be carried so far as to involve cell fusions such as Winkler believes preceded the formation of his *Solanum darwiniamum*. Even if this should not be proved, his experiments show beyond question the existence of graft-hybrids of a sort quite inconceivable in any animals except very low types, such as corals where it is by no means impossible that similar graft-hybrids might be developed.

It is this positive demonstration of the reality of "vegetative" or "somatic" hybrids which gives the experiments of Winkler their greatest value, and it is to be hoped that they will serve as a stimulus to other work in the same direction which may well have a great influence upon the drift of biological speculations dealing with the laws of heredity.

A DOUBLE HEN'S EGG[1]

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DOUBLE hens' eggs have always attracted much attention and the literature covering the records and descriptions of the various kinds has become extensive. In a comparatively recent paper published in this journal, Parker[2] has reviewed the main contributions to the subject and from a consideration of these, together with his own observations on five double eggs, has been led to the conclusion that at least two factors are involved in the production of such eggs. According to him, double-yolk eggs are produced when there is a simultaneous discharge of two yolks from the ovary, whether these are derived from a single follicle or from two separate follicles; while inclosed eggs may be the product of a normal ovary and probably are produced through the abnormal action of the oviduct, "in that a yolk normally supplied by the ovary may be abnormally covered, retained and inclosed in another egg." Parker therefore classifies the factors concerned in the formation of double eggs as ovarian and oviducal. Three types of double eggs result from the action of these two factors: (1) those in which the yolks have been derived from an abnormal ovary but have traversed a normal oviduct, (2) those produced by an ovary and an oviduct both of which have functioned abnormally, (3) and those in which the yolks have come from a normal ovary but have passed through an abnormal oviduct.

The egg described in the following pages clearly belongs to the third type, and since it possesses certain

[1] Contributions from the Zoölogical Laboratory of the University of Texas, No. 107.

[2] "Double Hens' Eggs," by G. H. Parker, AMERICAN NATURALIST, Vol. XL, 1906.

FIG. 1. A photograph of the egg. $\times \frac{2}{3}$.

FIG. 2. In this photograph the egg is shown after an incision had been made in the outer membrane and the upper margin of the cut turned back so as to reveal the inner membrane. Note that while the outer membrane shows deposits of lime, especially on the smaller end of the egg, the inner membrane, on the contrary, is entirely free from such deposits. $\times \frac{2}{3}$.

FIG. 3. This shows both membranes cut open and the contents of the egg clearly revealed. The dark mass lying just to the left of the inclosed egg is the yolk of the inclosing egg. $\times \frac{1}{2}$.

peculiarities that have not appeared in any previous account, seems to be worthy of record. It should be kept in mind, however, that the value of such descriptions does not come from the morphological features revealed, no matter how bizarre these may be, but from the fact that considerable light is often thereby shed on the complex physiology of the reproductive organs, and it is with this idea in mind that the following record is made.

The egg in question, which was kindly handed to me by Mr. S. L. Pinckney, Austin, Texas, was laid March 28, 1910. It was stated that several double eggs had been received from the flock from which this egg came, but whether they were all laid by the same hen could not be ascertained. The egg was large, measuring 85 mm. in its long axis and 62 mm. in the short axis, and was slightly smaller at one end than at the other, so that we may speak of the blunt and pointed ends. It was practically a soft-shelled egg, in that the amount of lime deposited on the shell-membrane was very small, and for the most part was collected into little nodules scattered about over the surface (Figs. 1 and 2). A microscopical examination of the shell-membrane did not reveal anything unusual, for it consisted of the two characteristic layers, a thick outer and a thinner inner; but on cutting it open I was surprised to find another shell-membrane lying almost directly beneath it (Fig. 2). The two membranes were separated by the very thinnest layer of watery albumen. This second or inner membrane was in every way normal, and perfectly white, but was entirely void of lime deposits, reminding one very much in its general appearance of the membranes on eggs which have just reached the isthmus.

The contents of the inner shell-membrane consisted of much albumen in which were imbedded a hard-shelled egg and a yolk (Fig. 3). Upon examination the inclosed egg was found to be perfectly normal in every respect, and its yolk contained a healthy blastoderm. The inclosed yolk, although normal in structure, was much dis-

torted, owing to the pressure exerted upon it by the approximation of the hard-shelled egg. The albumen closely adhered both to the egg and to the yolk, but much of it was of a liquid nature, as was indicated by the ease with which it flowed out of the cut first made in the inner membrane.

The accompanying diagram will make clear the relation of the various parts of this interesting monstrosity (Fig. 4). The inclosed egg lies toward the pointed end

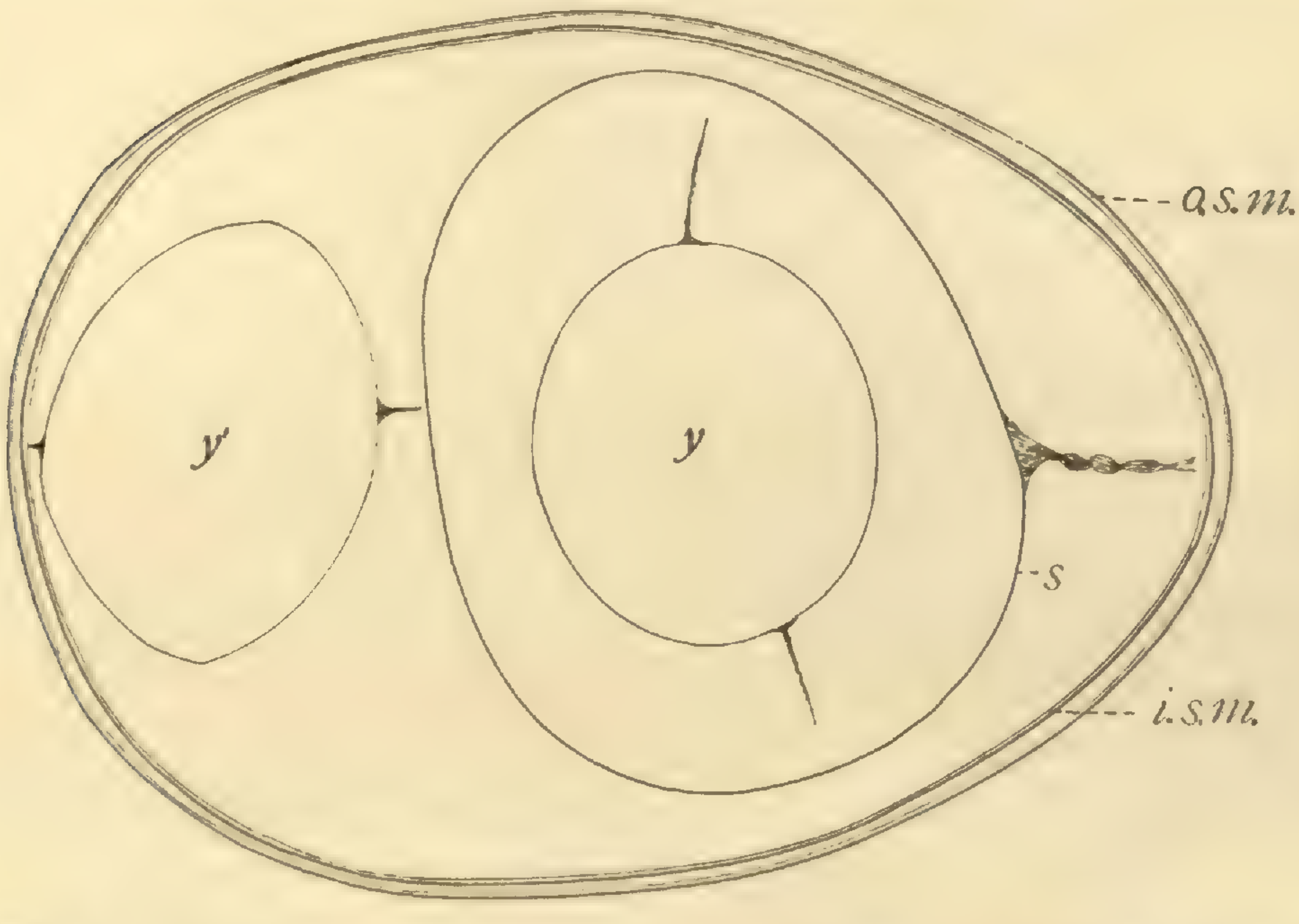

FIG. 4. Diagram of a median section of the egg. *i.s.m.*, inner shell-membrane, the two lines representing its two layers; *o.s.m.*, outer shell-membrane; *s*, shell of the inclosed egg; *y*, yolk of the inclosed egg; *y'*, yolk of the inclosing egg. Natural size.

of the inclosing egg, and its long axis meets the corresponding one of the double egg at an oblique angle. On account of this inclination of the inclosed egg its pointed end lies nearer to the blunt than to the pointed end of the inclosing egg. The inclosed yolk occupies the blunt end of the inclosing egg and is considerably distorted by pressure. The chalazæ are but poorly developed, but the axis formed by a line passing through their points of attachment to the vitelline membrane approximately coincides with the long axis of the inclosing egg, showing that the yolk has maintained its original orientation.

As I have pointed out above, the most interesting question regarding this egg pertains to the physiology of its formation. Parker states that two hypotheses have been advanced to explain how inclosed double eggs are formed. According to one of these, which was first advocated by Panum,[3] the inclosed egg remains in the distal part of the oviduct until overtaken by a second one, when both are then surrounded by a common envelope; according to the other a completely formed egg is carried by antiperistalsis back up the oviduct, where it meets a second one, and the two passing down become covered by a second shell and are laid. It seems quite evident from the description of the egg just given that it is the product of antiperistalsis, but the especial interest lies in the fact that this process has taken place twice.

The first antiperistalsis took place immediately after the hard-shelled egg was formed, and of course caused its migration to the upper or proximal end of the oviduct where it met the second egg. This meeting must have taken place very close to the infundibulum, for otherwise the yolk of the second egg would have possessed much larger chalazæ.

The second antiperistalsis occurred immediately after the inner of the two shell-membranes had been laid down, and must have succeeded in carrying the double egg up the oviduct to a point where albumen is secreted, that is, to a place slightly above the beginning point of the isthmus; for it is only on this assumption that we are able to explain how a thin layer of albumen came to exist between the two shell-membranes. The small amount of lime deposited on the outer of the two shell-membranes indicates that the egg did not remain long in the uterus, but must have been laid shortly after having entered that organ.

In many respects this egg conforms to the facts already seen in the inclosed types of double eggs; thus the in-

[3] Untersuchungen über die Entstehung der Missbildungen zunächst in den Eiern der Vögel,'' by P. L. Panum, Berlin, 1860.

closed egg lies near the pointed end of the inclosing one, and it was laid during the time of year when such eggs most frequently appear, that is, in the winter or spring; but it differed in one rather important respect. The pointed end of the inclosed egg does not lie in the same direction as that of the inclosing one. This unusual position of the inclosed egg doubtless has been brought about by crowding, and does not indicate necessarily that it was at first incorrectly oriented.

Among the more important things so far revealed by a study of inclosed double eggs is the light thrown on the problem of the orientation of the egg in the oviduct, a problem in which the writer has been deeply interested. These eggs clearly demonstrate that when an egg has once entered the oviduct its original orientation in that organ is maintained during the formation of the envelopes, no matter to what extent it may have been moved up and down the reproductive passage. This fact strongly supports the conclusion reached by the writer[4] in a recent contribution, in which it was pointed out that the definite orientation of the egg in the reproductive passage is not a matter of chance, but is something that is handed on to the oviduct by the ovary, that is to say that the ova in the ovary have a definite polarity which is passed on to the oviduct through the mechanism of the infundibulum.

[4] "The Early Development of the Hen's Egg, I., History of the Early Cleavage and of the Accessory Cleavage," by J. Thomas Patterson, *Journal of Morphology*, Vol. 21, 1910.

NOTES AND LITERATURE

HEREDITY

One of the most important papers relating to heredity that has appeared in recent months is that of Tower, dealing with hybridization investigations with species of the genus *Leptinotarsa*.[15] I shall not here attempt an extensive review of this paper, but mention it rather as a means of calling attention to its importance and suggesting that any one interested in theoretical discussions of heredity should not fail to read it. Tower has done an immense amount of work with this genus. His results lead him to accept the factorial hypothesis as an explanation of Mendelian phenomena but to discard wholly the de Vriesian interpretation of these factors. The most important contribution in this paper is the apparent fact that the environment at the time when eggs are fertilized may change very materially the nature of the hereditary factors. It is unfortunate that the author does not give more details in connection with this conclusion. The data he does give are mixed and contradictory. There has possibly been an error in printing Tower's paper, but if not there was a serious error in its preparation, as will be seen from the following. In experiment 409, which was several times repeated, the results were exactly as if one of the parents had been a heterozygote between the two species. F_1 consisted of two types, one of which was identical with the female parent and the other intermediate between the two. The one like the female parent bred true to that type, while the other behaved in all respects as a heterozygote. In experiment 410 the same two species were utilized, but the temperature and humidity conditions at the time the eggs were fertilized were made quite different. This experiment, which was repeated eleven times, gave in every case ordinary Mendelian phenomena.

In experiments 409/411, which was performed seven times, one set of eggs from the same cross as above was produced under conditions identical with those of experiment 409, and in

[15] Tower, Wm. L., "The Determination of Dominance and the Modification of Behavior in Alternative (Mendelian) Inheritance, by Conditions Surrounding or Incident upon the Germ Cells at Fertilization," *Biol. Bull.*, XVIII, No. 6, May, 1910.

each case gave identical results with those of 409; that is, F_1 consisted of two types, one heterozygote, and the other homozygote of the maternal type. Using the same individuals which produced a set of eggs of this kind to secure another set of eggs produced under the conditions of experiment 410, the results in each of the seven experiments gave F, which behaved in all respects as a homozygote of the maternal type. This fact is set forth in considerable detail and Plate III illustrates it just as here described. This result occurred in all cases whether the set of eggs produced under the conditions of experiment 410 was produced before or after the set which gave the results of experiment 409. Now the remarkable thing about this experiment is this. While in experiment 410 the results in each of the eleven cases gave ordinary Mendelian heterozygotes in F_1, in each of the seven cases of 409/411 the eggs produced under the same conditions as 410 gave homozygotes of the maternal type. Thus, the conditions of experiment 410 in eleven cases gave one result, in seven other cases they gave an entirely different result, and the only difference in the conditions was that in 409/411 the female either had produced or was in the future to produce a set of eggs under the conditions of experiment 409 (p. 295).

Thus, on page 294, in describing experiment 410, it is stated that experiment 410 gave F_1 all heterozygote; on page 330 it is stated that experiment 410 gave F_1 all homozygote of the maternal type; on page 295–6, in describing experiment 409/411, it is stated that, under the conditions of experiment 410, this experiment gave F_1 all homozygotes of the maternal type; and on page 304 it is stated that experiment 409/411, when performed under the conditions of 410, gave results identical with those of 410. These statements are directly contradictory. We must withhold judgment on this point of influencing the hereditary factors at the time of fertilizations, until Mr. Tower informs us which of these statements are correct.

In these exceptional cases, where the F_1 hybrid behaved as a homozygote of one of the paternal races, the author does not tell us whether the F_2 and later generations were each time produced under the conditions which produced the aberrant F_1. One would infer, however, that they were not, and that the change which occurred in the fertilization of the eggs which produced F_1 was permanent and not reversible. It is hoped

that he will give us fuller data on this point in future papers which are promised.

In several cases Tower mixed three species which interbred freely and left them under natural conditions for several years. A careful study of the progeny in each case showed that a new type arose, consisting of a complex of the characters of the old types, and that this new type rather rapidly replaced every other type, although some of these other types were known to be quite capable of existing under the conditions of the experiment. This would indicate that in some way the new type had a distinct advantage over the other types with which it competed for food, or possibly the repeated crossing of the types was in some way inimical to all the types except the one. Experiments of this character show that hybridization may be an important factor in the development of new varieties or possibly new species.

From the fact that when the same species are mixed together in two places where the conditions are different, the resulting type which finally wins out and becomes practically the sole representative of the mixture, is different under different conditions. Tower draws the conclusion that the conditions surrounding the germ cells at the time of fertilization "profoundly modify the behavior and the relationships of the characters entering into the crosses." This conclusion seems hardly justified. Of course it may be correct, but the well known fact that from complex crosses of this kind a great many types may result from what we know of the behavior of Mendelian characters and that these types would naturally bear different relations to the environmental conditions offers apparently a much simpler explanation of the reason for the survival of the one type under one set of conditions and another type under another set of conditions. It seems hardly necessary to assume that the conditions existing at the time of the fertilization of the egg determine the characters which were to result from the fertilization to explain this particular phenomenon.

Subsequent investigation of these new types of mixed origin showed that in all cases they occasionally produced individuals different from the general population but which in all cases exhibited characters which were present in the original parents of the complex mixture. Tower repeatedly compares this phenomenon to the phenomena which de Vries observed in *Œno-*

thera lamarckiana, and suggests that the mutations which de Vries observed are probably due to previous hybridization. This is a very interesting suggestion, but the writer is inclined to believe that the phenomena observed by de Vries were due to a different cause. It is definitely proved that in some of de Vries's mutants the chromosome numbers are different from those of the parent form. Cytological investigations have also shown that in the reduction division in these *Œnothera* mutants there are frequent irregularities in the distribution of chromosomes. It seems probable that de Vries's mutations are not the result of previous hybridizations but rather are due to irregular behavior of chromosomes in the reduction division. If this is true then the phenomena observed by de Vries would be due to a different cause from that which presumably produced the results which Tower observed. In the case of Tower's results we can explain the facts by the assumption of simple Mendelian segregation. In de Vries's work there is evidence that the phenomena are due to a different cause.

It is gratifying that Tower takes a very broad view of the factorial hypothesis of Mendelian phenomena. On page 323 he remarks:

> This factorial point of view is in no wise, of necessity, to be tied to or confounded with such speculations as the id-determinant-biophore fabric of Weismann, nor with the pangene complex of de Vries, which have no foundation in fact.

This is the view which the writer has held for years and has frequently set forth in these pages. I have also frequently pointed out that we do not yet have sufficient knowledge of the physiological processes of living matter to permit us at the present time to formulate an adequate theory of the phenomena observed in hybrids. I think we can, however, point out the general nature of the causes underlying these phenomena, as I have attempted to do in my theory of Mendelian phenomena.[16] In speaking of the difference in germ cells with respect to given characters, he has the following to say:

> What this difference in the gametes is we do not know, but observed behaviors are interpreted as being, most probably, due to the mechanical separation into different germ-cells of whatever it is that produces the contrasting attributes—segregation during gametogenesis.

[16] *American Breeders' Magazine,* Vol. I, No. 2.

He further remarks on page 328:

> At present in biology we have no business with ultimate conceptions, and the two thus far attempted of germinal composition—the "particulate conception" and the "crystalline entity" are both equally dismal failures and equally useless as working hypotheses.

The statement on page 335, that characters which Mendelize are in the main unimportant attributes of the organism and only rarely are of importance in the struggle for existence, is a little bit strong. Apparently it would have been better to state that those characters which have been shown to Mendelize are of this nature. Unfortunately, most of the work of the Mendelians has been done with these superficial, easily observed characters. I see no reason why any character whatever might not, from the failure of some chromosome to perform a usual function, give a variation which would behave in Mendelian fashion if the resulting type were capable of propagating and crossing with the parent type.

Tower's paper will undoubtedly have an important influence on biological thought, as it deserves to have.

W. J. SPILLMAN.

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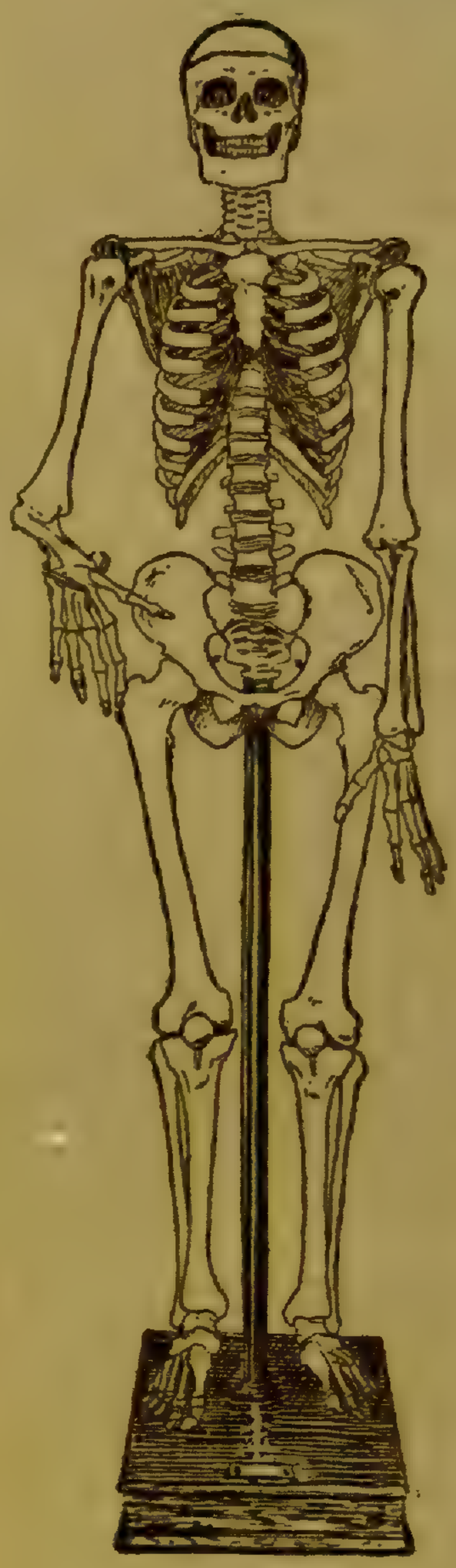

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Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

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THE
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THE APPLICATION OF THE CONCEPTION OF PURE LINES TO SEX-LIMITED INHERITANCE AND TO SEXUAL DIMORPHISM[1]

PROFESSOR T. H. MORGAN

COLUMBIA UNIVERSITY

IN the same sense in which our ideas concerning variation and heredity have been entirely revolutionized since 1891, so has a similar change taken place in regard to our theories of sex determination. Sex is now treated by the same methods that are used for Mendelian characters in general. From this point of view I propose to consider to-day three questions, intimately associated. First, the treatment of sex as a Mendelian character; second, the relation between sex and the inheritance of secondary sexual characters; third, the bearing of the recently discovered cases of "sex-limited-inheritance" on the problem of the transmission of characters in general.

Most modern theorists are in agreement that the heredity of sex can be best understood when one sex is regarded as a pure line, or homozygous, and the other sex is treated as a phænotype, *i. e.*, as heterozygous. The experimental evidence has made it plain that in some animals and plants it is the female that is heterozygous, and in other animals and plants it is the male that is heterozygous. Hence have arisen through the necessities of the situation the two following classes of formulæ:

[1] From a symposium on "The Study of Pure Lines of Genotypes," before the American Society of Naturalists, December 29, 1910.

	Gametes	
	♀	♂
♀♂ Female		
♂♂ Male	♂	♂
	♀♂	♂♂
	female	male

	Gametes	
	♀	♀
♀♀ Female		
♀♂ Male	♀	♂
	♀♀	♀♂
	female	male

In certain groups of animals, as in *Abraxas* amongst insects, and in poultry amongst birds, the first scheme is essential to an interpretation of the facts obtained by experiment. In other groups, as in *Drosophila* amongst insects, and in man amongst the vertebrates, the second scheme accounts for the experimental results.

These methods of formulation are open to two serious objections. As the tables show, the combination of ♀♂ stands for the female in one case, and for the male in the other. In order to avoid this apparent contradiction it is assumed that in some groups femaleness dominates maleness, and in other groups maleness dominates femaleness, which seems to me paradoxical at least.

It will be observed also that in the first of these schemes the male carries none of the sexual characters of the female, and in the second scheme the female carries none of those of the male; both of which assumptions do not seem to me to be completely in accord with fact. Cytologists represent these same two schemes in a different way. They represent in the one case the female character by X; and the male by the absence of X. Thus:

	Gametes	
	X	O
XO Female		
OO Male	O	O
	XO	OO
	female	male

This representation covers the first class of cases where the female is heterozygous. For the second class, where the female is homozygous, the following scheme is

used, in which the female is represented by two X's and the male by one X:

	Gametes	
XX Female	X	X
XO Male	X	O
	XX	XO
	female	male

The XO—OO scheme applies, as before, to the case of *Abraxas* and to poultry, and the XX—XO scheme to the other class of cases. The latter expresses also exactly what takes place in the chromosomes of those groups where two classes of sperm exist (in relation to the X element), as has been demonstrated by Stevens and by Wilson.

In both of these two latter schemes the production of the female is ascribed to the presence of the chromosome X, but in the first formula one X makes the female and its absence stands for the male, while on the second formulation two X's make the female, while one makes the male. In one case XO is female and in the other XO is male. Again we meet with the same paradox as in the first two formulations.

The chief drawback to these formulæ is, in my opinion, the absence of any character to stand for maleness. Absence of femaleness does not appeal to me as a sufficient explanation of the development of a male; for the male is certainly not a female minus the female characters.

Nevertheless, despite these objections I am inclined to think that these two methods of formulation indicate the direction in which we must look for an explanation of the experimental evidence, and that they may be still utilized provided we can so modify them that their inconsistences can be made to disappear.

It seems to me that if we are to succeed in bringing sex into line with Mendelian methods we must be prepared to grant that there are representative genes for the male condition and others for the female; and we must so shape our formulæ that the female carries the

genes for the male and the male carries those for the female. In fact, I am inclined to think that the evidence forces us to accept Darwin's original view, that in each sex the elements of the other sex are present; a view that has been largely given up by modern theorists (except by Strasburger). I think that we must accept this interpretation for several reasons. Every zoologist is familiar with cases in which the same individual may at first function as a male and later as a female. More remarkable still is the case of the Nematodes in which in some species the female has come to produce both eggs and sperm as shown by Maupas and more recently by Potts, while in another closely related species it is probably the male, according to Maupas and Zur Strassen, that has come to produce eggs as well as sperm. There is further the class of cases where the female develops the male secondary characters and the male those of the female. This class of cases I shall discuss later, for the value of this evidence will turn on whether these secondary sexual characters are represented by independent genes, or are expressions of the presence of one or the other sexual condition; or due to a combination of these two possibilities.

By means of the following formulæ we can meet the requirements that the situation seems to me to demand. If we admit that in the first class one of the genes has become larger than the other female genes, and if we admit that in the second class one of the female genes has become smaller than its sister genes we can account for the results as the following formulæ show:

		Gametes	
Fmfm	Female	Fm	fm
fmfm	Male	fm	fm
		Ffmm	ffmm
		female	male
FmFm	Female	Fm	Fm
Fmfm	Male	Fm	fm
		FFmm	Ffmm
		female	male

It should be carefully observed that in this scheme the female genes, F or f pair when they meet (allelomorphs); likewise the male genes pair only with male genes. In fact, both genes are carried by all of the gametes. Sexual dimorphism may appear either because one female gene has become stronger than the others, or, because one has become weaker. On the first view we have the case where the female is heterozygous in its female genes; in the latter case it is the male that is heterozygous in its female genes. If in this latter case we assume that the weakened female gene is contained in the so-called Y-chromosome we can then understand how it is that we have a degraded series of this chromosome leading in some forms to its final extinction, for even its disappearance leaves the formulæ unaffected. On the same grounds we may anticipate that in those species in which the X elements are alike in the male, one X in the female may be found larger than its partner, although visible size differences in the chromosomes are not essential to the scheme, since these chromosomes undoubtedly contain many other factors than those of sex whose presence might obscure size relations even when such exist in the sex genes.

These formulæ appear more complicated than those previously given, but in reality they are not so. It is the presence of m in all of the gametes that gives the appearance of complication. If this is omitted, as in the formula given below, the formulæ are no more complex than those given earlier.

		Gametes	
Ff	**Female**	**F**	**f**
ff	**Male**	**f**	**f**
		Ff	**ff**
FF	**Female**	**F**	**F**
Ff	**Male**	**F**	**f**
		FF	**Ff**

The formulæ might be further simplified, if it seemed desirable to do so, by simply indicating the determining factor in each case as shown below; thus:

		Gametes	
FO	Female	F	O
OO	Male	O	O
		FO	OO
OO	Female	O	O
Of	Male	O	f
		OO	Of

But this last simplification is misleading, if the thesis that I shall here maintain in connection with sex-limited inheritance is correct; because the F's and the f's omitted in the last case are supposed to be carried in definite bodies, the chromosomes, which also carry other factors than sex factors, and it is essential to indicate their presence in some way in order that these other factors may have some means of transportation.

In a recent paper on sex determination in phylloxerans and aphids (1909) I discussed at some length different theories of sex determination, and adopted provisionally the view that the outcome is determined by a quantitative factor. The present hypothesis is little more than a further development of this same view,[2] but I hope in a form more in accord with the Mendelian treatment of the problem. Sex is still represented as the result of a quantitative factor F (or f), but its relation to the male factor is now expressed, for maleness is not assumed, as before, to be no femaleness or less femaleness. Here, as there, more of a particular factor turns the scale towards femaleness in the first class of cases, and less of the female factor allows the scale to turn in the opposite direction in the second class of cases.[3]

[2] In 1903 I suggested that in the case of the bee a quantitative factor determines sex, viz., the chromatin; two nuclei producing a female and one a male. Wilson (1905) has identified the quantitative factor with a special chromosome and this interpretation of the quantitative factor is here followed. On Wilson's view the male condition is represented by the absence of the X-chromosome in some cases, and by the presence of only one X-chromosome in the others, (see ante); but on my view the determination of sex is regulated by this quantitative factor in relation to another factor, the male determining element.

[3] It should be pointed out that these formulæ are in no way related to a suggestion that I made in 1907 in regard to dominance and recessiveness

These formulæ have certain advantages over those now in vogue, first, because the male gene is not ignored as a factor in sex determination; second, that its presence, both in males and females, explains how under certain conditions the male or the female may assume some of the characters of the opposite sex; third, that the paradox of the female being the heterozygous form in one class and the male in the other class is, in part at least, resolved; fourth, that the ease with which species pass from the hermaphrodite condition to that of sexual dimorphism and the reverse is understandable; fifth, that the production of males by parthenogenetic females can be accounted for by the loss of one of the female genes in the polar body; and lastly, we see how there may be two kinds of eggs, as in *Dinophilus apatris*, both of which can be fertilized; for, in such cases the spermatozoa should be all alike.

I do not wish to urge this view too positively, for I am acutely aware that we are only at the beginning of our understanding of the problem of sex determination, but I believe that the difficulties of the current hypotheses must be clearly understood and met if possible.[4]

The Inheritance of Secondary Sexual Characters

From the point of view reached in the preceding discussion let us now examine the problem of the inheritance of secondary sexual characters.

Males are distinguished from females not only by the presence of sperm in place of eggs, but by the presence

in general. That view I have entirely abandoned. In the present hypothesis the relation of the determining elements is stated in the same form as in other Mendelian formulæ, with the possible exception that here one gene is represented as larger or smaller than its allelomorphs, and the scale is turned by the mass relation between these female genes and those of the male.

[4] I have not discussed here the possibility of selective fertilization, because if we can explain the facts without this problematical assumption we simplify the problem greatly. Moreover, the evidence brought forward by Payne, Brown and myself, while admittedly insufficient, stands definitely opposed to the view of selective fertilization.

of different kinds of ducts, glands, copulatory organs, or other accessory sexual apparatus; and also by structures not essential to reproduction. These last we call the secondary sexual characters.

It has long been known that in the embryonic development of the vertebrates some of the accessory organs of the male appear in the female, and conversely some of the accessory organs of the female in the male. This evidence seems to me to point with no uncertain meaning to the conclusion that each sex carries the genes of the other. It is however the secondary sexual characters rather than these accessory organs of which I wish to speak now; for, these often appear to be present in one sex only. Are these characters represented in all eggs and sperm or are they by-products of the sexual condition of the animal? Fortunately there is a good deal of experimental evidence that bears on this question, but it is also true that the evidence teaches that the matter must be handled with care, and if I seem to speak dogmatically it is for lack of time rather than for want of caution.

It has been shown by Meisenheimer that removal of the gonads of the caterpillar of *Ocneria dispar* fails to produce any effect, or very little, on the secondary sexual characters of the moth. It would seem, therefore, that these characters are represented in the germ cells in the same way as are other characters, and are not dependent for their development on the presence of the gonads. Some mechanism must exist by means of which the genes of these organs are distributed so that two kinds of individuals are produced. It has been suggested by Castle that the secondary sexual characters may be carried by the Y-element in the formulæ XX = female, XY = male, but this hypothesis fails to explain the results when the Y-element is absent, as E. B. Wilson has pointed out. It also fails to explain how the male secondary sexual organs can appear in the female after castration.

On the sex formulæ that I have suggested it is possible to account for the results, if the genes for these

characters are carried by all cells alike; possibly they go along with the male-group, but this is not essential. Whether they *develop*, or not, will depend on the presence of other genes in the cells. Thus when the Fmfm group is present they will be suppressed, or when, as on the other formulæ, the FmFm group is present. We can understand on this view why in the insects the male secondary sexual organs do not develop in the female after removal of the ovaries, because in this group it is not material derived from this source, but from materials produced in the cells themselves, that bring about the suppression.

It has been demonstrated by Geoffroy Smith that when the young males of the spider crab, *Inarchus mauretanicus*, are infested by *Sacculina* the secondary sexual characters of the female develop. It appears that the parasite produces some substance that inhibits the activity of the male-producing group in each cell, or counteracts some materials produced there, so that the female characters now find the situation favorable for their development. When the young female crab is infected by *Sacculina* she does not develop the male secondary characters, which is in harmony with the view just stated for the manner of action of the parasite.

In birds and in mammals it has long been recognized that some substance is produced in the ovary that inhibits the development in the female of the male secondary sexual characters, for, after removal of the ovaries the male characters may *to some extent* develop. It seems fairly clear that here the female group in each cell fails to entirely suppress the male characters; the inhibiting effect from this source must be reinforced from something produced in the ovary. Whether after castration of the male the secondary sexual characters of the female develop is not so clear, since some at least of the characters that characterize the castrated male may be juvenile. But on my view the possibility exists for the castrated male to produce the secondary sexual

characters of the female, if their development is in part suppressed by substances made in the testis.

The view here presented also allows us to explain how the secondary sexual characters of the male are transmitted through the female, as they may be so transmitted.

THE INHERITANCE OF SEX-LIMITED CHARACTERS

In recent years a new class of facts has been discovered that promises to throw a flood of light not only on the sex-determination problem, but also on the problem of inheritance in general. I refer to the cases of sex-limited inheritance.

We mean by sex-limited inheritance that in certain combinations a particular character appears in one sex only. An example will make this clear. In one of my cultures of the red-eyed fly, *Drosophila*, a white-eyed male appeared. Bred to red-eyed females, all of the offspring, male and female alike, had red eyes. These inbred produced red-eyed males and females, and white-eyed males. In other words the white-eyed mutant transmitted his character to half of his grandsons, but to none of his granddaughters.

Yet this white-eyed condition is not incompatible with femaleness; for, it can be artificially carried over to the female by making a suitable cross. If, for instance, a white-eyed male is crossed with a heterozygous red female, there will be produced red-eyed males and females and white-eyed males and females.

There are certain combinations of sex-limited characters that give results outwardly similar to sexual dimorphism. If a black langshan cock is crossed to a dominique hen, all of the sons are barred and all of the daughters are black. If a white-eyed *Drosophila* female is crossed with a red male all of the sons will have white eyes, and all of the daughters will have red eyes. I have another strain of these flies with *small wings* and still another strain with *truncated wings*. If a female of the former is crossed with a male of the latter strain all of

the daughters will have *long wings* and all of the sons will have *small wings*, like their mother.

These cases conform to Mendel's principle of segregation. Were there time I could show by an analysis of the problem why these sex-limited characters behave in inheritance in a different way from secondary sexual characters, although the results in both cases may be accounted for on the assumption that there are genes in the cells for both kinds of characters. In a word, this difference exists because one of the factors for the sex-limited characters in question is absent from one of the *female determining chromosomes*, while the genes for the secondary sexual characters of the male are contained in other chromosomes, possibly in those that contain the male determinants.

This interpretation of the relation between the X-chromosomes and sex-limited characters makes it now possible to demonstrate a point of great theoretical importance. I invite your serious attention for a few moments longer to this question. Three other characters have appeared in my cultures that are sex-limited; one of these only I may now speak of. A male with wings half the normal length suddenly appeared. He transmitted his short wings to some of his grandsons, but to none of his granddaughters. I tried to see if the other sex-limited character, white eyes, could be combined in the same individual with short wings. As the next diagram shows a red-eyed short-winged male was bred to a white-eyed female with normal wings. All of the offspring had long wings; the female had red eyes and the males white eyes. These were inbred and produced white and red-eyed males and females with long wings, red-eyed males with short wings, and white-eyed males with short wings. In the last case the transfer had been made. The reciprocal cross also given in the diagram is equally instructive.

LWF — LWF Long-winged, white ♀
SRF O Short-winged, red ♂

LWFSRF — LWF

LWF SRF SWF LRF ♀ Gametes
LWF — O ♂ Gametes

LWFLWF Long-winged ♀ white eyes
SRFLWF Long-winged ♀ red eyes
SWFLWF Long-winged ♀ white eyes
LRFLWF Long-winged ♀ red eyes
LWF Long-winged ♂ white eyes
SRF Short-winged ♂ red eyes
SWF Short-winged ♂ white eyes
LRF Long-winged ♂ red eyes

LRF LRF Long-winged, red ♀
SWF O Short-winged, white ♂

LRFSWF — LRFO

LRF SWF LWF SRF ♀ Gametes
LRF O ♂ Gametes

LRFLRF Long-winged ♀ red eyes
SWFLRF Long-winged ♀ red eyes
LWFLRF Long-winged ♀ red eyes
SRFLRF Long-winged ♀ red eyes
LRF Long-winged ♂ red eyes
SWF Short-winged ♂ white eyes
LWF Long-winged ♂ white eyes
SRF Short-winged ♂ red eyes

In both cases the combination is possible because in the female of the hybrid (F_1) a shifting of the gene for long and that for short wing (both carried by the X-chromosome) takes place. This interchange is possible during the synezesis of the two X-chromosomes. On the other hand the male contains only one X-chromosome which has no mate, hence the gene for long wings in the hybrid (F_1) can not leave that chromosome to pass into the male-producing group. If it could do so short-winged females would also appear, but as I have shown they are not present in the second generation.

Interpreted in terms of chromosomes these results can have, in my opinion, but one meaning. During union of homologous chromosomes (during synezesis, perhaps) homologous genes pair and later separate to move to op-

posite sides (or enter the chromosome sometimes one way and sometimes the other). All the genes contained in the X-chromosomes can thus shift in the female because in this group two X's are present. Sex-limited inheritance is only possible where similar conditions exist (either in the male or in the female) and since in man color blindness follows the same scheme as does white eyes in my flies, we have an experimental proof that in the male of homo sapiens there is only one X-chromosome, and this, in fact, Guyer has just shown to be the case from cytological evidence. But by parity of reasoning it is the female in Gallus bankiva that should have only one X present, but Guyer is persuaded that here too (at least in the race of fowls he studied) the male has only one X-chromosome. There is then in this case a contradiction between the experimental evidence and that furnished by cytology and it remains to see which is correct.

Bateson has shown that some of these cases of sex-limited inheritance can be explained on the grounds that there is a repulsion between the female-determining factor and that character that is sex-limited. The view that I maintain does not involve the idea of a repulsion between unlike elements, not allelomorphic. Spillman's hypothesis also involves this idea of repulsion between unlike elements. On my view, on the contrary, an attempt is made to show how the results may be due to a connection existing between certain material bodies in the egg; a connection that is consistently carried through successive generations, and subject only to the ordinary interchange of genes between homologous chromosomes (when a pair of chromosomes is present).[5]

For several years it has seemed to me that the chromosome hypothesis, so called, could not be utilized to explain the Mendelian results in the form presented by

[5] The hypothesis advanced here to explain sex-limited inheritance applies also to Abraxas if the latter follows the Fmfm scheme and if ***in the egg*** there is no interchange between the F-bearing and the f-bearing chromosomes.

Sutton, because, if it were true, there could be no more Mendelian pairs in a given species than the number of chromosomes present in that species. Even if this objection could be avoided[6] the more serious objection still remained, namely, that with a small number of chromosomes present many characters should Mendelize together, but very few cases of this sort are known. De Vries was the first, I believe, to point out that this objection could be met if the genes are contained in smaller bodies that can pass between homologous pairs of chromosomes; and Boveri has admitted this idea as compatible with his conception of the individuality of the chromosomes. In the case of the inheritance of two sex-limited characters in the same animal we have an experimental verification of this hypothesis.

[6] Spillman's suggestion that the difficulty exists only when it can be shown that more dominant characters can occur in the same individual than the number of chromosomes seems to me only to push back the difficulty.

PURE LINES IN THE STUDY OF GENETICS IN LOWER ORGANISMS[1]

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AT the meeting of this society a year ago I asked in a paper read,[2] whether the pure line idea did not deserve agitating a little before this society, and I tried to agitate it. This was because I saw that for practical purposes of future work it would be necessary to make up my mind as to the importance of this idea, and it seemed that other members of the society might be in the same situation and that we might help one another. My method of agitation was to give the apparent relations of the results of work along this line up to that time, to one of the burning problems in our field—the problem of selection. In the few minutes that each of us have here the purpose of agitation can be served and general results brought sharply into view only by naked and dogmatic statements, such as one would never use under other conditions. Such naked and dogmatic presentation has serious disadvantages—felt most decidedly by the author when his critics hold the mirror up to nature. I have therefore at times regretted giving forth this paper. But if it has in any way acted as an irritant to arouse the discussion foreshadowed in our present program, I shall feel that its good results outweigh its painful ones, and that it was worth while after all. We are apparently to have brought before us a part of that "thorough try out" that I asked for, and from a study of our program I think I can see that it is not all to be a pæan of praise for the pure line work. Such illumination and such interest as comes

[1] From a symposium on "The Study of Pure Lines or Genotypes," before the American Society of Naturalists, December 29, 1910.

[2] This JOURNAL, March, 1910.

from having both sides presented I believe that we have before us.

What I wish to attempt is to give some concrete illustrations of the answer to the question discussed by Dr. Webber—What *are* genotypes? I note that some of the titles on our program speak of the genotype *hypothesis*, the pure line *theory*. What I wish to emphasize is that these things, whatever we call them, are concrete realities —realities as solid as the diverse existence of dogs, cats and horses. I find in many biologists not working in genetics an incorrigible bent for seeking under such a term as genotype something deeply hypothetical or metaphysical, and for characterizing it therefore boldly as purely imaginative. This is merely because such workers have not the things themselves before them. The genotype is merely a race or strain differing hereditarily in some manner from other races. Neither the idea nor the fact is a new one, and we should perhaps do better to discuss merely the importance of distinguishing in our work the diverse existing strains—rather than to introduce an unfamiliar term for a familiar thing. But investigation has shown the existence of these strains to play a part of such hitherto unsuspected importance that it has seemed worth while to introduce a more precise term, which shall emphasize their importance for work in genetics. In work with a certain lower organism—*Paramecium*—I have found the existence of these diverse strains or genotypes to be the guiding fact, not only for work in genetics, but for all exact work in comparative physiology. I wish to show how this is true.

We must then distinguish clearly these concrete realities called genotypes from any theories that have been built up in connection with them; from any generalizations based on their study up to this time. The existence and importance of genotypes are not bound up with any particular theory regarding selection or any other single point. In lower organisms, at least, genotypes or pure lines are merely the name for certain actual existences that you have before you; for facts that strike you

in the face. We *have*, side by side in the laboratory, a lot of diverse sets of our organisms, each set derived originally from one individual, and each differing characteristically but minutely from the others—the differences persisting from generation to generation. The behavior and properties of these things are of course a matter for further study. Can selection change them? Can environmental action permanently modify them? These are matters quite distinct from the existence of the genotypes.

To get a clear grasp of the matter, I believe that those not working with lower organisms will find it worth while to try to realize the condition which the investigator in this field has before him. A comparison may help. In lower organisms the genotype is actually isolated, each in a multitude of examples, which live along without admixture, visibly different from all others, for many generations, before again plunging into the melting pot of cross-breeding. In higher organisms we should have the same thing if every rabbit, every dog, every human being, multiplied by repeated division into two like itself, till there were whole counties inhabited by persons that were replicas of our absent president; cities made up of copies of our secretary, and states composed of duplications of the janitor I saw outside. Every human being, as it now stands, represents a different genotype (save perhaps in the case of identical twins), and these genotypes become inextricably interwoven at every generation. It is therefore easy to see how the genotype idea might appeal to workers among higher organisms as a mere hypothesis.

What then are these visible, tangible, isolated genotypes (or races, or strains) of lower organisms, and how are they distinguished? Taking *Paramecium* as a type:

1. Some of them differ in size—the size of each remaining closely constant, under given conditions, for hundreds of generations; for years. This was the first difference observed, and I tried to demonstrate it by giving measurements of successive generations of the different races. But to the worker in the laboratory these differences are evident without refined measurements; the student is at

once struck with the fact that one culture is formed of individuals that are throughout and constantly larger than those of another culture.

And here, in view of that extraordinary cry "no heredity without a correlation table"[3] (a cry that at once annihilates most Mendelian evidence of heredity), it may be well to define a little more precisely what is meant by saying that the diverse sizes are hereditary in the different races. It means that if you keep your different genotypes side by side under precisely the same conditions, you will find whenever you choose to examine and measure them, that each has a characteristic size, differing from that of the others. If therefore you follow the diverse lines from generation to generation you will get a set of chains, each with links differing characteristically throughout from the links of the other chains. It means that it is possible to predict the diverse relative sizes that will be found in the different races, and that when you examine them a hundred generations later, you will find the prediction correct. These striking facts *are what are meant* by the statement that the diverse sizes are hereditary in the different lines—and the way to determine whether the statement is true or not is to examine the lines from generation to generation to see if the statement is verified. To neglect this obvious fact; to mix all your lines together and then, in order to find out if size is inherited, to laboriously work out coefficients of correlation by refined biometrical methods—is like cutting serial sections ten microns thick of an eel, in order to find out whether it has an alimentary canal. Persons have been known to so bedevil material with refined histological methods as to quite miss the alimentary canal of an eel. The way to see it is to open the animal up and take a look at it. The way to see diverse genotypes is to isolate them and look at them and measure them and compare them. If the use of correlation tables should succeed in obscuring these striking facts (as should not be the case with proper handling) this would merely show the worthless-

[3] Compare Pearson, *Biometrika*, 1910, Vol. 7, p. 372.

ness of this method of attempting to learn the important biological facts under consideration.

2. Some of the genotypes show slight but constant differences in structure, which I shall not dwell upon here.[4]

3. They show most varied differences in their physiological characters. These physiological differences may go with differences in form and structure, or apparently they may not—so that we find types that differ, so far as detectable, *only* in physiological peculiarities.

This fact becomes of great practical importance for all physiological investigations, as a few examples from *Paramecium* will show:

(*a*) The races or genotypes differ in the conditions, both external and internal, that induce conjugation. A worker, using a certain strain, works out the conditions inducing conjugation and gives precise directions for accomplishing this. His colleague, with another strain, finds this work all wrong, and the controversy on this ancient question continues. One of my strains can be absolutely depended on to conjugate monthly if certain definite conditions are furnished; another under the same conditions never conjugates; others show intermediate conditions. These differences require no biometric methods for their demonstration.

(*b*) Again, the genotypes differ in rate of multiplication; under the same conditions some divide once in twelve hours; others once in twenty-four or more hours; others have intermediate periods.

(*c*) The genotypes differ as to the conditions required for their existence and increase. Several strains, outwardly alike, living in the same medium, are cultivated side by side on slides, in the usual hay infusion. One flourishes indefinitely. Another multiplies for ten generations, then dies out completely, and this is repeated invariably, no matter how many times we start anew our

[4] For a detailed, illustrated account of the characters, both structural and physiological, of these races, see Jennings and Hargitt, "Characteristics of the Diverse Races of *Paramecium*," *Journal of Morphology*, December, 1910.

cultures of this genotype. A third lives along in a sickly way, barely maintaining its existence.

Thus we get in our laboratory striking cases of natural selection between genotypes. To recall our comparison with human beings, if we could mix an entire community composed homogeneously of, let us say, Roosevelts, with another of copies of your ash man—which would be likely to survive? If we place together in the same culture two genotypes of *Paramecium*, as I have many times done, almost invariably one flourishes while the other dies out. This ruins many a carefully planned experiment; it must take place on a tremendous scale in nature.

What distinguishes the different genotypes then is, mainly, *a different method of responding to the environment*. And this is a type of what heredity is; an organism's heredity is its method of responding to the environmental conditions. Under a given environment the genotype *A* is large, while the genotype *B* is small. Under a given environment the strain *C* conjugates, while *D* does not. Under a given environment the strain *E* divides rapidly, *F* slowly or not at all. The various strains thus differ hereditarily in these respects, and we may say that the differences are matters of heredity. And yet we can get these same contrasts within any genotype (as our diagram illustrates), by varying the environment. The genotype *A* under one environment is large; under another it is small. Under one environment the type *C* conjugates; under another it does not. Under one environment *E* divides rapidly; under another, slowly. Are then size, conjugation and rate of fission after all determined by heredity or by environment? Such a question, when thus put in general terms, is everywhere an idle and unanswerable one. All environmental effects are matters of heredity when we compare types differing in their reaction to the environment; all hereditary characters are matters of environmental action when we compare individuals of the same heredity under effectively different environmental conditions.

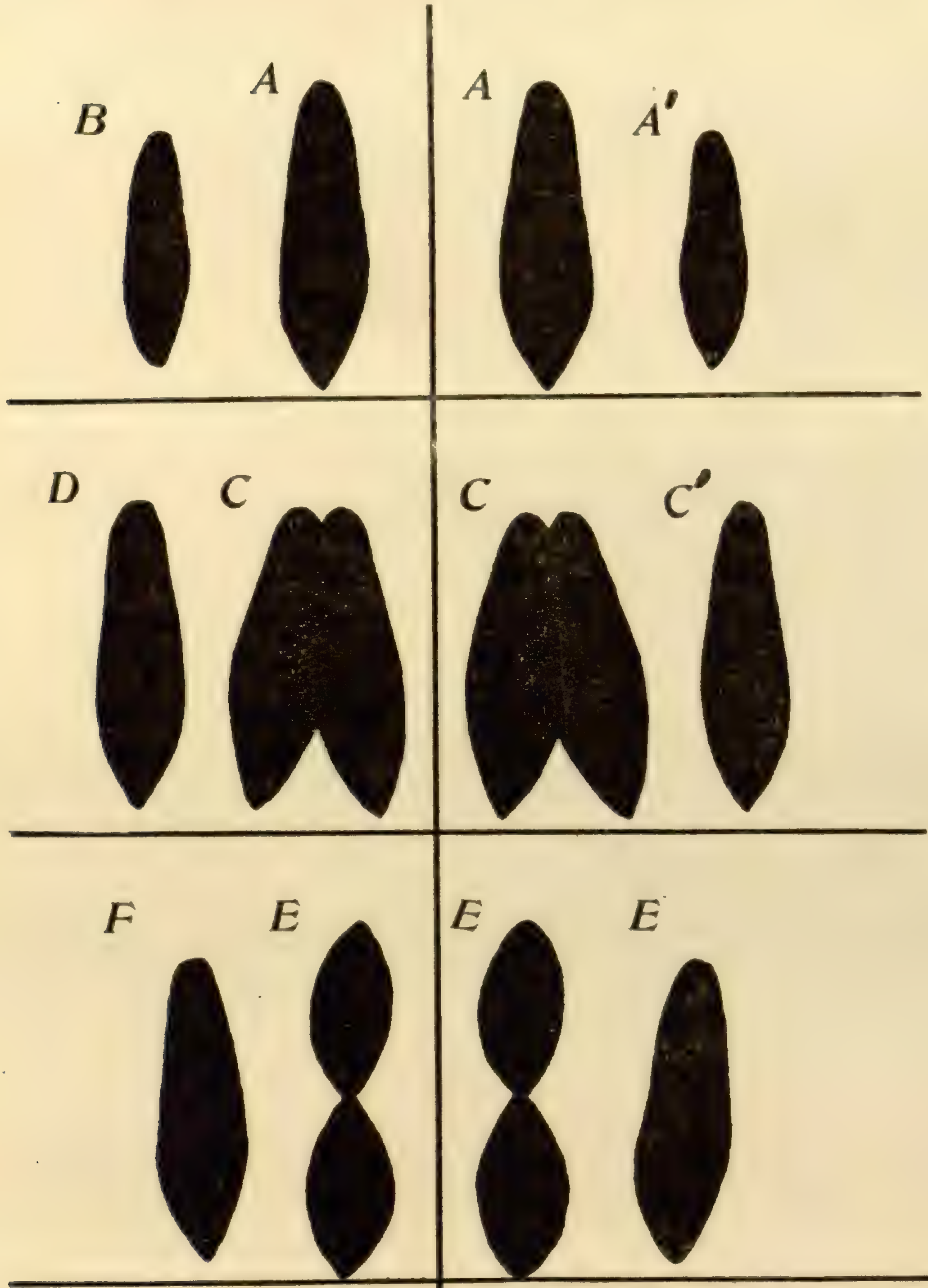

DIAGRAM TO ILLUSTRATE THE RELATION OF HEREDITY TO ENVIRONMENTAL ACTION IN DETERMINING CHARACTERS. (See text.)

Heredity has a meaning only when we (explicitly or implicitly) compare two concrete cases; when we say: To what is due the *difference* between these two cases? Otherwise we can demonstrate either that all character-

istics are hereditary (as we heard maintained at Woods Hole some summers ago); or, with Brooks, that there is no such thing as heredity. If we always compare two concrete cases, asking to what is due the difference between them, and remembering that a difference in heredity means different response to the same environment, we shall avoid these confusions, and shall find the concept of heredity most useful.

Do hereditary differentiations ever arise within our genotypes, so that from one genotype we get two? In other words, do we get from a single type strains that differ in their behavior under the same environment—the differences persisting from generation to generation? This is of course one of the fundamental questions. The genotypes of *Paramecium*, like those of most other organisms that have been carefully studied, are singularly resistant, remaining quite constant in most respects, so far as has been determined. This is an example of what gives the genotype concept its practical and theoretical importance. This is what is meant by saying that selection and environmental action are usually without inherited effect within the genotype. To find differentiations within the genotypes of *Paramecium*, we must examine certain characteristics that are most delicately poised in their responses to all sorts of conditions; such is the rate of multiplication. Studying carefully this most sensitive character, we find that differences do arise within the genotype. Under given conditions, certain rare individuals are found that divide more slowly than usual, others more rapidly, and these differences are perpetuated from generation to generation indefinitely. How are these hereditary differentiations produced?

The origin of these differentiations is in *Paramecium* as elusive as in most other cases where they have been discovered. Apparently they arise in our organism as a result of conjugation within the genotype. Certainly if after an epidemic of conjugation within the genotype we cultivate many isolated exconjugants, we find a certain small number of strains that differ in their rate of fission

from that which is typical. But the experimental analysis of this matter is still in progress, and conclusions can not yet be drawn.

It is only in rate of multiplication that I have thus far found hereditary differences arising within the pure line, and these but rarely. But this encourages one to hope that the same may be found for other characters when these are extensively studied with sufficient minuteness. The negative results thus far reached do not (as many critics have pointed out) exclude the possibility that rare cases of hereditary variation within the pure line will yet be found. What the negative results have demonstrated is that a very large share of the observed variations in organisms are not hereditary, and that selection based on these variations leads to no result—a conclusion of such great importance as to make the pure line work epoch-marking in character.

Finally, what happens when diverse genotypes mix in conjugation? To my disappointment, I have found this much more difficult to determine for the infusorian than I expected. This is owing to the fact that the conditions for conjugation differ in the diverse genotypes, so that it is almost impossible to get them to conjugate at the same time. Further, in the rare cases where two are conjugating at once, the assortative mating discovered by Pearl results in the two sets remaining separate. Thus I have not yet been able to get crosses between two genotypes whose characteristics are known beforehand; and this will be necessary before a study of inheritance, exact in the modern physiological sense, can be made. On the other hand, it *is* possible to get conjugations in wild populations that include many genotypes, and to compare the results with conjugations where but a single genotype is involved. Certain most interesting results appear. In these conjugations of mixed populations, a great number of diverse combinations are produced; the variability increases greatly, in size and in other respects. Numbers of the strains produced die, or multiply so slowly that they have no chance in competition with

those that are strong and multiply rapidly. Thus many of the combinations produced are canceled; only the strongest combinations survive. We have then on a most extensive scale an operation in natural selection and the survival of the fittest; the production of many combinations, some of which survive, while others fail. As already set forth, there is some indication of the same process in the case of conjugation within the genotype.

At our last meeting I tried to summarize the facts as to the relation of genotypic investigation to selection; it turned out that much which had been deemed a progressive action of selection was not such; and up to that time the action of selection in modifying genotypes had not been demonstrated. Similarly, I had earlier summarized the facts regarding selection in behavior, showing that it there plays a large part. I have hence suffered the peculiar fate of being belabored as an anti-selectionist in genetics, while subjected in the field of behavior to rough treatment as the champion of selection. What I tried to do in both cases was, to determine how far we had actually *seen* the effectiveness of selection—holding this question quite apart from what we believe *must* occur, or believe will be found to occur when we have seen it. It appeared clear, and still appears clear, that a very large share of the apparent progressive action of selection has really consisted in the sorting over of preexisting types, so that it has by no means the theoretical significance that had been given to it. When operating on a single isolated type it appeared that the progressive action of selection had not been seen. These are facts of capital importance to the experimenter; besides their theoretical significance, they open to each of us the opportunity to direct our efforts upon precisely this point, and so perhaps to be the first to see examples of this fundamental process not yet seen. I hoped to accomplish this myself, but after strenuous, long-continued, and hopeful efforts, I have not yet succeeded in seeing selection effective in producing a new genotype. This failure to discover selection resulting in progress came to me as a

painful surprise, for like Pearson I find it impossible to construct for myself a "philosophical scheme of evolution" without the results of selection and I would like to see what I believe must occur. It is therefore with some pleasure that I am able to record for *Paramecium* this extensive operation of selection among the diverse existing lines, and particularly in this extensive production of new combinations at conjugation, with cancellation of many of the combinations. It would seem that the diverse genotypes must have arisen from one, in some way, and when we find out how this happens, then such selection between genotypes will be all the selection that we require for our evolutionary progress. What I hope, therefore, is that some one on our program, more fortunate than myself, will be able to record seeing the actual production of two genotypes from one, or the transformation of one into another, by selection, or in any way whatever.

Yet even if this is done, we shall make the greatest possible mistake if we therefore conclude that the existence of genotypes is unimportant, and throw the matter aside; for work with a mixture of unknown genotypes will always give confused and ambiguous results, whose significance no one can know. If on the other hand we work with single genotypes, or with known combinations of them, we shall understand what our results mean. And this applies to work in other fields of biology as well as to genetics.

SOME EFFECTS OF TEMPERATURE UPON GROWING MICE, AND THE PERSISTENCE OF SUCH EFFECTS IN A SUBSEQUENT GENERATION[1]

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I MUST preface my remarks by an apology for coming before you with some results which have already been published pretty fully within the past year.[2] My appearance here may seem the more unwarranted in view of the limited amount of evidence which I am about to offer upon those subjects which form the focus of attention at this meeting, namely heredity and evolution. However, aside from the fact that I am acting at the instance of our president, I will say two things in my own defense. First, the results which I offer, meager as they doubtless are, appear to be the only ones of just this sort which are in evidence at present.[3] And secondly, I am bold enough to believe that I have developed a promising method of attacking a few of the many knotty problems which are bound up together in the time-honored question: Are

[1] Read before the American Society of Naturalists, December 30, 1910.

[2] "Some Effects of External Conditions upon the White Mouse," *Journal of Experimental Zoology*, August, 1909. "The Reappearance in the Offspring of Artificially Produced Parental Modifications," AMERICAN NATURALIST, January, 1910. "An Experimental Study of Somatic Modifications and their Reappearance in the Offspring," *Archiv für Entwicklungsmechanik der Organismen*, June, 1910.

[3] Since writing this statement, I have received Semon's highly interesting paper, entitled 'Der Stand der Frage nach der Vererbung erworbener Eigenschaften" (Fortschritte der naturwissenschaftlichen Forschung, Bd. II, 1910). From this I learn that some of the more important features of my results have been obtained by Przibram, in the course of experiments upon rats, conducted at about the same time as my own. I have not yet seen Przibram's own report of his work. This confirmation will, I trust, dispel any doubts as to the statistical significance of my own figures, whatever interpretation we may choose to give them.

acquired characters inherited? It is my hope to convince you that the method which I have employed conforms to certain *a priori* requirements, on the one hand, and, on the other hand, is workable in practise. That my results are not thus far more imposing is due, I think, to no defect in the method itself, but to the limitations which encompass a solitary investigator, deprived of some of the generally acknowledged desiderata for successful work in animal breeding, such, for example, as assistants, funds and adequate equipment.

As to the logical requirements for such a test—to begin with, what is it that we are going to test? The "inheritance of acquired characters"?—yes and no. First of all, that threadbare expression itself must be relegated to limbo where it belongs. For, not only does it fail to indicate with any precision the subject-matter of our inquiry, but historically the expression has been applied to a wide range of phenomena, real and alleged. Some of these we now know to be fictitious; others, on the contrary, are acknowledged facts; while others yet are more or less debatable. It is with the debatable group, of course, that we are here concerned. But, even among these, we encounter not one problem but many. Suppose, then, that we drop all vague generalized expressions and consider one more or less restricted problem: *Are specific structural effects, resulting from the action of external conditions upon organisms of one generation ever repeated in the next generation under such circumstances that the immediate and parallel modification of the germ-cells may not be invoked as an explanation?* Under "specific structural effects," I do not wish to include general conditions of health, metabolism, etc.

What are some of the necessary conditions for a fair test of this question? To begin with, we must effect our modifications in the first generation. And since these modifications, if repeated at all, will probably reappear in a much-diminished degree, it would seem far preferable to select characters which lend themselves readily

to accurate measurement. Qualitative differences, such as those of color or of physiological reactions, do not seem well adapted to such experiments, although they have commonly been the ones dealt with in studies of this sort.

In the second place, we must choose such an organism and such a physical agency that the latter may act upon the former without immediately influencing the germ-cells. This would seem to rule out of consideration as really crucial tests of this problem all experiments, however instructive otherwise, in which modification has been brought about through the influence of foods, unusual in amount or in character. For the effect of these upon the parent body is, of course, a chemical one, and the specific substances responsible for the modifications are presumably free to enter the germ-cells. The experiments of Arnold Pictet upon lepidoptera and of Houssay upon fowls are to be recalled in this connection. Similar considerations apply with equal force to any results from experiments in which invertebrate animals or "cold-blooded" vertebrates have been influenced by temperature. The recent work of Kammerer upon lizards[4] and that of various investigators upon butterflies and moths occur to us at this point; likewise certain features of Tower's work on *Leptinotarsa*. In such cases, by pretty general consent, we have to do with an "immediate effect upon the germ-plasm," and not with *transmission* at all. Later, I shall inquire a little into the validity of this assumption.

In the meantime, I will point out that for certain classes of animals this objection cannot be raised, at least in its original form. I refer to the so-called "warm-blooded" ones. I am not very well versed in that branch of physiology which deals with temperature regulation, but the published evidence which I have examined seems to show that mammals normally undergo but slight fluctuations of body temperature as a result of even very

[4] *Archiv für Entwicklungsmechanik der Organismen*, September, 1910.

considerable changes in the temperature of the surrounding atmosphere.[5]

Assuming, provisionally, the truth of this proposition, we may discount in advance the objection that the germ-cells of a mammal may be influenced by differences of temperature *as such*. If these differences affect the germ-cells at all, and it is reasonable to believe that they may do so, they must act upon them indirectly.[6] I shall revert to this point again shortly.

As some of you may perhaps already know, I have succeeded for several years past in producing very decided quantitative differences in certain of the external parts of mice through the action of widely differing temperatures. . . . (This part of the discussion has been omitted in the printed report, since the results in question have already been fully published.)

In experiments such as those which I am describing, it is obviously impossible to subject a single individual to both extremes of temperature during growth, and to compare the differing effects of these upon structure. We therefore, of necessity, resort to a comparison of averages, based upon as many individuals as possible. If each of the contrasted groups is sufficiently large, and if its members have been taken at random, the presumption

[5] Przibram found that the body temperature of his rats was somewhat raised when kept in a room at 30° to 35° C. This last was, however, considerably higher than the mean temperature of my own warm room, and the limits of physiological adaptability seem to have been overstepped in his experiments. (See Semon, *op. cit.*, pp. 45, 46.) On the other hand, Pembrey (*Journal of Physiology*, 1895) found that the body temperature of mice did not rise appreciably above the normal when the animals were kept at a temperature of 29.5° or even 32.5° C. for an hour or more. The effects of a more prolonged stay were not determined. I have myself recently commenced experiments with mice, using a special clinical thermometer made for the purpose. I have already (January 21) shown pretty conclusively that mice may have almost precisely the same rectal temperature at —6° C. as at + 30° C.

[6] The same is true even if humidity, rather than temperature *per se*, is the factor chiefly concerned in these modifications. As stated in my first paper (1909), the relative humidity of my heated room was very much lower than that of the unheated room. Thus far I have not differentiated the effects of these two factors.

is that the mean potential (that is to say, congenital) value of every character is about the same for the two lots. I fully realize that the study of genetic problems by the use of mass averages has recently received a decided set-back, largely through the labors of some of those who have contributed to our present program. But until some one is ingenious enough to produce a strain of parthenogenetic or self-fertilizing mice, I fear that my only practical method of procedure in these experiments is to deal with mass statistics based upon "heterozygous" stock.

It must also be pointed out that the technique of the problem which I am discussing is inevitably different from that involved in the endeavor to find, or to produce, "mutations" or single abrupt deviations from the parent stock, which appear at once in full force, if they appear at all, and thereafter breed true. On the contrary, the distribution of the lengths for the tail, ear and foot, within each of the temperature groups in my experiments, appears to follow the normal probability curve, just as in the case of the so-called "fluctuating variations," whose heritability is nowadays so much in question.

In the splendid paper of Professor Johannsen, to which we listened yesterday, occurs the following statement: "as yet no experiment with genotypically homogeneous cultures has given any evidence for the Lamarckian view, the most extreme 'transmission'-conception ever issued." Leaving aside for the time being the question whether results such as mine, even when every possible defect of technique has been eliminated, are to be regarded as "evidence for the Lamarckian view," let us consider for a moment whether the fact that I have not myself found it practicable to use "genotypically homogeneous cultures" does, in reality, invalidate the evidence which I offer. Apparently Professor Johannsen would hold this to be true. So far as I can see myself, the only difference between results from pure and from mixed lines in the

present case would be this. Individuals belonging to a single pure line would probably respond with much greater uniformity to the effects of an environmental change than would those belonging to a composite stock, consisting of a number of lines. It is quite conceivable that among these last some would respond in a much greater measure than others. Or indeed some might not be affected at all. But here the much-scorned "mass statistics" would reveal the mean tendencies of the two lots, and the resulting data, though confessedly capable of further analysis, would be none the less valuable. If it be objected that the differences between the two averages may be due to the presence in one or both of the contrasted lots of a few "mutants," while the remaining individuals may not have been affected at all, I will only point out, as above, that the frequency distributions are directly opposed to such an assumption.

Having produced modifications of the sort mentioned, it remained to be seen whether these effects persisted beyond the generation immediately influenced. . . . (This part of the discussion, including an account of the method employed, the results, and certain of the possibilities of interpretation, I have thought it best to omit here, in view of the fact that I have covered practically the same ground in statements already published. I will merely note that the offspring of warm-room and cold-room mice, although themselves reared under identical temperature conditions, presented differences of the same sort as had been brought about in their parents through the direct effect of temperature, viz., differences in the mean length of tail, foot and ear.)

There remain two principal alternative explanations, which are not wholly distinguishable from one another, and neither of which admits of being stated except in rather vague terms.

One of these is the assumption that the changes undergone by the parent body are in some way registered in the germ cells, so as to be repeated, in a certain measure, in

the body of the offspring. This conception has taken various forms, commencing with Darwin's hypothesis of "pangenesis." The same general view has recently been restated in chemical terms, and in a manner which is perhaps far less shocking to our common sense.

The other alternative is that of a "parallel induction" or "simultaneous modification of the germ-plasm," through the direct action of the modifying agent. This explanation, as we all know, has been freely used by Weismann and others to account for a considerable range of phenomena, notably the persistence of temperature effects in a second generation of butterflies. The phrase has indeed become so familiar through long repetition that few of us stop to consider just what it implies. "Parallel modification of the germ-plasm?" How can the unformed material of the germ cells be modified in the same manner as certain groups of somatic cells—say in a butterfly's wing—even by an all-pervading influence like temperature? This is obviously not what is intended. What we mean, concretely stated, is this: the germinal matter is so affected by the temperature that, after some hundreds or thousands of cell generations, certain of the resulting cells will show peculiarities in their pigment-producing powers of the same nature as those which arose directly in the somatic cells of the parent. And a most curious feature of this coincidence is that these modified cells are situated in precisely the same parts of the body in the one case as in the other.[7]

Thus do these very simple explanations have a way of losing their simplicity when examined critically. In the present instance, the hypothesis stated may, for all we know, be the one that most nearly represents the truth. But it should be stated frankly, in all its complexity, and not palmed off upon us as a readily intelligible hypothesis, which relieves us of the necessity of adopting an "inconceivable" one such as that of pangenesis.

[7] Weismann's "determinant" hypothesis offers at least a *formal* solution of this difficulty, but I think that most biologists will agree with me that the solution thus offered is almost wholly a formal one.

In the case of a warm-blooded animal, of course, such an explanation as the foregoing could not be offered without still further modification. It might be conceded that temperature, as such, could not affect the germ-cells to any appreciable extent. But it might, on the other hand, be contended that the effects of temperature, even upon the parent body itself, may not be direct, but may be due to the formation of specific chemical substances, which, through the medium of the blood, may be supposed to simultaneously influence the body and the germ-cells. Thus we should, after all, be invoking a "simultaneous modification of the germ-plasm," as in the case of cold-blooded animals.

Such a conception, vague as it is, has certain decided elements of strength. Let me point out, however, as I have already done more than once, that any such chemico-physiological mechanism as is here assumed would be of nearly or quite the same value for evolution as the "inheritance of acquired characters" in the old sense. An interpretation of this sort might "save the face" of certain speculative students of heredity, but the difference between the two views would have little but academic interest.

At the present time, I am continuing these experiments with mice, and am not only using much larger numbers than hitherto, but am resorting to several variations of the original theme, by which I hope to reduce the number of possible interpretations to a minimum. A friend wrote to me recently, wishing me no end of "good results, *not Lamarckian.*" This doubtless represents the attitude of a large number of persons toward the whole subject. By many, anything with a taint of "Lamarckism" about it would seem to be, *ipso facto,* beyond the pale of legitimate scientific investigation, belonging rather to the same category as pre-natal influences, telepathy and the "borderland" phenomena of psychical research. But the dawn of better times is already with us.

In conclusion, let me state that my own attitude toward

this group of problems is one of indecision. If I confess to you, as I am bound to do, that positive results from my own experiments will give me far greater satisfaction than negative ones, this is chiefly because negative results commonly prove nothing. The question would be left very nearly as it was before. This, of course, constitutes a serious defect in my own vaunted method of attacking the problem, a defect which it shares, however, with any other which could be devised. But any results are better than no results, and these problems seem worth a far more thorough testing than they have yet received. The present experiments ought, as Professor MacDougal has pointed out,[8] and the author keenly realizes, to be subjected to various checks and controls, and to be continued through a considerable series of generations. It is my own fervent hope to be able to carry out such a program.

[8] Presidential address before the American Society of Naturalists, read at Ithaca, December 29, 1910.

THE MENDELIAN RATIO AND BLENDED INHERITANCE[1]

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The indefatigable efforts of neo-Mendelists have succeeded in bringing numerous cases of inheritance, which had previously been considered incompatible with Mendel's law, into their domain by widening the original limitations. We still have many instances such as blended inheritance which can not apparently be harmonized with the law of Mendel. Recent experiments which demonstrate the existence of various degrees of dominance as well as the mutability of the determinants in their behavior, suggested to the writer that various forms of inheritance might be considered as degrees of modification of the law of Mendel. With this view in mind, I have attempted to obtain some general expression for the underlying principle of the law of inheritance by which means Mendel's original law may possibly be theoretically connected with the other cases. In fact, I was compelled to pursue this investigation in connection with my own experiments on the inheritance of the weight of the central nervous system, though this is not yet ready to present at this time.

In carrying out this investigation, I have assumed that the germ plasm is composed of many factors, the true nature of which is unknown, but which in one way or another determine the characters in the offspring. It is these hypothetical factors which are here provisionally called determinants. With this understanding, we may now proceed to the argument.

Suppose a gamete of one parent after the reducing division contains n determinants, the whole group of

[1] Read before the American Society of Naturalists, December 30, 1910.

determinants being designated p, and the gamete of another parent also contains after the reducing division n determinants, the whole group being designated q. Then in the first hybrid zygote (F_1) there will be contained at the time of the union of the gametes $2n$ determinants. As we know, rearrangement takes place during the maturation of the germ cells and we assume this rearrangement to involve a random sampling by which n determinants are taken from the group of $2n$. From the theory of probabilities we find that n, $n-1$, $n-2$ . . . determinants of either parent contained in the gametes of F_1 are proportional to the successive terms of the following series:

$$p^n + np^{n-1}q + \frac{n(n-1)}{1\cdot 2}p^{n-2}q^2 + \frac{n(n-1)(n-2)}{1\cdot 2\cdot 3}p^{n-3}q^3 + \cdots \quad (1)$$

The same phenomenon happens in the gametes of the other hybrid parent (F_1) and since the gametic constitution of the two hybrid parents is assumed to be identical with respect to the distribution of determinants (1), the frequency of the various combinations of the determinants in the second hybrid offspring (F_2) will be given by the square of (1) or

$$\left(p^n + np^{n-1}q + \frac{n(n-1)}{1\cdot 2}p^{n-2}q^2 + \frac{n(n-1)(n-2)}{1\cdot 2\cdot 3}p^{n-3}q^3 + \cdots\right)^2 \quad (2)$$

which may also be written as follows:

$$(p^2 + 2pq + q^2)^n.$$

This series, or the square of the binomial series, is then the most general expression for the gametic composition of any hybrid arising from a combination of p and q determinants and may therefore be considered as the underlying principle of any law of inheritance where the idea of determinants is used.

It is evident that since the somatic characters in question depend entirely on the behavior of the determinants, the relative frequency of various zygotes, as well as the character of the zygotes, depends on whether p or q de-

terminants are related as dominant and recessive, respectively, or whether they blend.

Suppose p is recessive and q is dominant in the Mendelian sense, we at once obtain from (2) the general expression for the alternative inheritance or

$$(RR + 2DR + DD)^n$$

where n refers to the number of allelomorphic pairs of characters, and the expansion gives a strict Mendelian ratio for any number of allelomorphic pairs of characters.

On the other hand, if we consider that p and q determinants blend with an equal intensity the series (2) will give all grades of hybrid characters between the two parental types, the frequency of which is proportional to the successive terms of a symmetrical point binomial curve, and the maximum frequency will be associated with the midparental types (case of equipotency). Castle's ('09) experiments with the length of the ear of rabbits illustrates this case.

Again let us suppose that p and q determinants blend, but with unequal intensity. According as p or q is prepotent, the zygote will resemble more closely one or the other parent. The frequency of each type of zygote again will be represented by the symmetrical point binomial curve. Thus the present series (2) represents both alternative and blended inheritance according to the behavior of the determinants.

The fact just mentioned, that the expressions for both blended and alternative inheritance are obtained from the same series which represent the gametic composition, suggests that we may possibly obtain cases of blending in character which normally follow the law of the alternative inheritance, and vice versa, and further we may even obtain both blended and alternative inheritance in the same offspring by subjecting the hybrid parents to different conditions, provided by such treatment we can modify the behaviors or functional activity of the de-

terminants, since as soon as the behavior is altered, we at once obtain from the series (2) another type of inheritance.

Although we have no clear direct evidence which demonstrates an occurrence of such extreme modification in the behavior of determinants, nevertheless the possibility of such an event is amply suggested by the recent experiments. For instance Tower ('10) has shown not only a reversal of dominance and apparent failure of segregation by merely modifying the environment of the beetles, but also a case in which the same parents produce offspring, some of which follow the law of Mendel while others show entirely different behavior with respect to dominance and segregation. Tennent ('10) was able to obtain from a cross of *Hipponoë esculenta* with *Taxopneustes variegatus*, reversal of dominance by decreasing the alkalinity of the sea water. Numerous samples of this sort can easily be found in the recent literature.

Whatever be the real condition or conditions which control the behavior of the determinants, one point is clear from the above, that the determinants are not immutable in their behavior, but subject to modification. This fact naturally leads us to think that we may obtain various forms of inheritance which are more or less different from the type form according to degree of functional modification. When a modification is maximum, we may even obtain a case of blended inheritance in a character which normally follows the law of alternative inheritance, or vice versa.

The facts mentioned above then indicate that our deduction from the properties of the formula is not at all improbable.

Again the properties of the formula suggests that we can theoretically connect cases of blended inheritance with those of alternative inheritance by the mere assumption that p or q fails to dominate either completely or incompletely. Since as we have shown by the degree

of dominance, the formula reduces to either equipotent or prepotent blending inheritance. From this standpoint we may consider that blending inheritance is a limiting case of alternative inheritance where either dominance is absent (equipotency) or is imperfect (heteropotency). If this hypothesis is accepted, then Mendel's law of alternative inheritance may be taken as the standard, and all cases referred to it or blending inheritance (though by this some more important features of inheritance are not suggested) may similarly be made the standard, the Mendelian ratios then becoming a special case.

In this connection Professor Davenport's ('07) view on the law of potency is of great interest. As his view of potency is so important, and especially as it clearly explains the relation between Mendelism and cases considered to be non-Mendelian, I shall quote his words at some length.

After quoting various cases of inheritance, Professor Davenport says:

> Taking all cases into account, it is clear that Mendel's law does not cover all; and if not, it must be a special case of a more inclusive law. Can we find a more general expression for the inheritance of characteristics which will cover all these cases? I think we can and that it may be called the law of potency. At the one extreme of the series we have equipotent unit characters, so that when they are crossed, the offspring show a blend, or a mosaic between them. At the other extreme is allelopotency. One of the two characteristics is completely recessive to the other. Between the two extremes of equipotency and allelopotency lies the great mass of heritable characteristics which when opposed in heredity, exhibit varying degrees of potency. This sort of inheritance may be called heteropotency.

Thus Professor Davenport shows also that Mendelian dominance is a particular case of potency, allelopotency, though he did not state that blending inheritance is a limiting case of Mendelism.

Whether a new expression "the law of potency" should be introduced as Professor Davenport has suggested, or whether the various potencies may be consid-

ered as a limiting case of Mendel's law of alternative inheritance, thus saving the original name, is a matter for later decision, though the latter name seems to me more appropriate to retain owing to the fact that the phenomenon of segregation, most important of all, had been first stated by Mendel.

Let us now consider a limiting case of our formula (2) when the values of n (number of allelomorphic pairs of characters) increase. In the typical Mendelian ratio, the relative frequency of the various zygotes with respect to any given visible character is proportional to an expansion of $(1+3)^n$ which is the same as $(1/4+3/4)^n$ if we consider the relative values of the frequencies. Thus in all known cases of the inheritance, we have to deal with an expansion of $(r+s)^n$ where $r+s=1$. A concise mathematical formula which represents a limiting case of the binomial series arising from an expansion of $(r+s)^n$ will be very useful, especially when we are dealing with a quantitative measurement such as weight, length, area, volume, etc., since in these cases the values of the variates will be graded. Further, the theoretical frequency corresponding to each variate when the value of n becomes very large, can best be determined from such a mathematical expression which represents a limiting case.

Without going into any detail of the mathematical treatment, it will be seen that we obtain two forms of expression according as $r=s$ or $r \neq s$. The former will be represented by the normal probability curve and the latter by a limiting case of a skew binomial curve. For representing a skew binomial curve we can best use DeForest's formula (Professor Pearson's curve of type 3). It may be useful to the reader to know that DeForest's formula degenerates into the normal probability curve as its simplest form, as will be seen below.

DeForest's formula (Hatai: '10) is usually written in the following form:

$$y = \frac{1}{k\sqrt{2\pi b}}\left(1 + \frac{x}{ab}\right)^{a^2b-1} e^{-ax},$$

where

$$k = 1 + \frac{1}{12a^2b} + \frac{1}{288(a^2b)^2} + \cdots.$$

a = quotient of twice the second moment divided by the third moment.

b = second moment.

Writing c for

$$\frac{1}{k\sqrt{2\pi b}}$$

we have

$$\log\left(\frac{y}{c}\right) = (a^2b - 1)\log\left(1 + \frac{x}{ab}\right) - ax$$

$$= (a^2b - 1)\left\{\frac{x}{ab} - \frac{1}{2}\left(\frac{x}{ab}\right)^2 + \frac{1}{3}\left(\frac{x}{ab}\right)^3 - \frac{1}{4}\left(\frac{x}{ab}\right)^4 + \cdots\right\} - ax$$

$$= -\frac{x^2}{2b} + \left(\frac{x^2}{3b} - 1\right)\frac{x}{ab} - \left(\frac{x^2}{4b} - \frac{1}{2}\right)\left(\frac{x}{ab}\right)^2$$

$$+ \left(\frac{x^2}{5b} - \frac{1}{3}\right)\left(\frac{x}{ab}\right)^3 - \cdots.$$

Since for a vanishingly small value of the third moment, ab will be a very large number, consequently x/ab will be infinitesimal. Thus neglecting all terms in which x/ab is factor, we have

$$y = ce^{-\frac{x^2}{2b}}.$$

Restoring the value of C and remembering that for large values of ab, k reduces to unity, we finally have

$$y = \frac{1}{\sqrt{2\pi b}} e^{-\frac{x^2}{2b}}$$

which is the familiar formula for the normal probability curve.

From the above it is clear that DeForest's formula and its limiting case represent the frequency distribution of the zygotes, whether we are dealing with alternative or

blended inheritance. One, however, must not be misled to conclude that continuous variation necessarily means failure of segregation, since on the contrary apparent continuity may be a resultant of combinations of various segregating characters. Whether or not given data indicate a segregation, may be variously tested by some other means according to the nature of the experiment.

From the above we draw the following conclusions:

1. The series obtained from the square of the binomial expresses the distribution of determinants for both alternative and blended inheritance.

2. Blended inheritance may be considered to be a limiting case of alternative inheritance where dominance is imperfect. Thus Mendel's law of alternative inheritance may be considered as the standard and all other cases referred to it.

3. DeForest's formula with its limiting case adequately represents frequencies of all known cases of inheritance when the number of allelomorphic pairs of characters is large, especially when quantitative measurements are considered.

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DATA ON THE RELATIVE CONSPICUOUSNESS OF BARRED AND SELF-COLORED FOWLS[1]

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I. PHYSICAL DATA

THE purpose of this note is to put on record a rather striking physical fact, and to discuss briefly its biological significance. Some two years ago Davenport[2] published a short note regarding the relative number of self-colored and of "penciled or striped" chicks killed by crows one afternoon, at Cold Spring Harbor. The rather striking result was that out of 24 birds killed, only one was other than self-colored. The communication closes with the following words: "This fragment, then, so far as it goes, indicates that the self-colors of poultry, which have arisen under domestication, tend to be eliminated by the natural enemies of these birds, and the pencilled birds are relatively immune from attack because relatively inconspicuous."

Some photographs taken on the poultry range of the Maine Experiment Station this past summer illustrate this point made by Davenport as to the relative conspicuousness of self-colored birds in so striking and complete a manner as to warrant their publication and a critical discussion of their significance. These photographs were made without any thought whatever at the time that they were going to bring out the relative conspicuousness of different plumage patterns. Indeed, it was not realized that they did so until the finished prints were given to me by the station photographer, Mr. Roy-

[1] Papers from the Biological Laboratory of the Maine Experiment Station, No. 23.

[2] Davenport, C. B., "Elimination of Self-Coloured Birds," *Nature*, Vol. 78, p. 101, 1908.

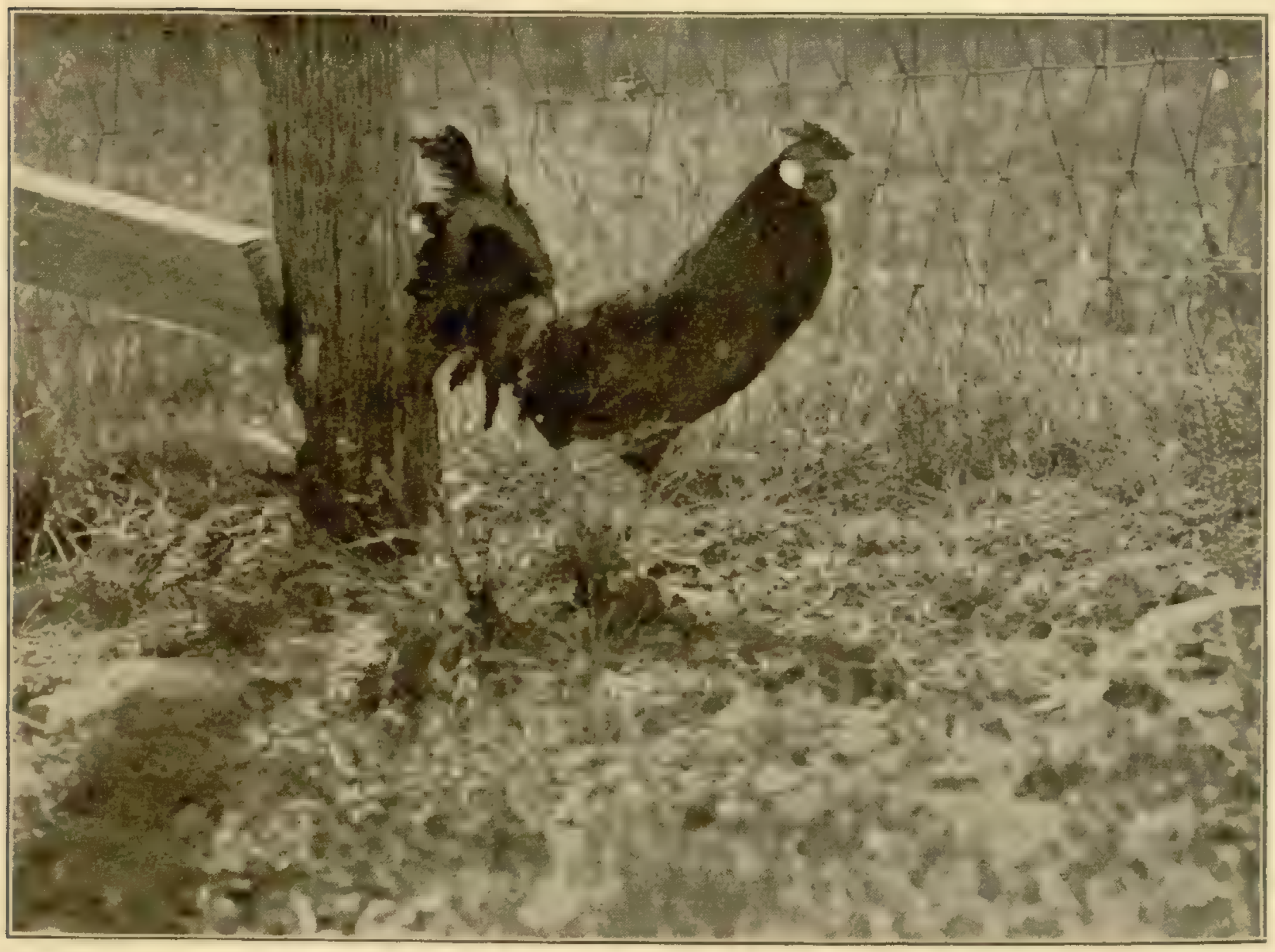

FIG. 1. Photograph of a Golden Pencilled Hamburg ♂. Practically a solid colored bird (red on body, black tail). The few barred feathers which the ♂ of this variety has are covered by solid colored feathers. In this picture one barred feather shows in the region of the saddle. The wind had displaced this feather.

den Hammond, to whom I am indebted for developing and printing these pictures. As a matter of fact the four pictures which accompany this note were taken for the purpose of (*a*) testing a then new camera as to its usefulness in obtaining pictures to form part of a permanent record system in poultry-breeding experiments, and (*b*) to get photographic records of certain particular birds of interest from one standpoint or another. All the exposures were made by the same person (the writer) on the same afternoon and within an hour of each other. It was on a cloudless afternoon early in August, and the light conditions, shutter-opening, speed, and diaphragm opening were constant for all of the pictures. What differences appear in the pictures, then, are such as are referable to the different color patterns of the birds, when seen under the light conditions and against the kind of background which obtained in this case.

FIG. 2. A very dark, practically solid black F_2 ♂ from the cross Cornish Indian ♂ × Black F_1 ♀ from Cornish Indian ♂ × Barred Rock ♀.

From these photographs the following points are to be noted:

1. As compared with self-colored birds the barred individuals obviously are relatively much less conspicuous, when under the same light conditions, and when seen against the same kind of a background. The pictures of the barred birds (Figs. 3 and 4) are not, to be sure, like the "puzzle" pictures of supposedly protectively colored organisms, which one sometimes sees, where it is exceedingly difficult to distinguish the animal from the background at all. In both Figs. 3 and 4 it is easy enough to see the bird, but at the same time these birds are obviously much less conspicuous than those shown in Figs. 1 and 2.

2. This inconspicuousness is equally marked whether the barred bird is in the bright sunlight (Fig. 3) or in a relatively deep shadow (Fig. 4).

3. These pictures furnish objective and unbiased phys-

FIG. 3. An F_2 barred cross-bred chick. Sex ♀. Produced by mating F_1 barred cross-breds *inter se*.

ical evidence regarding the relative conspicuousness of two types of plumage pattern.

II. DATA ON THE BIOLOGICAL VALUE OF THE INCONSPICUOUSNESS OF THE BARRED PATTERN

The physical fact set forth above is obvious: barred chickens are clearly less conspicuous than self-colored when seen against the background of grass on the range where they live. Has this physical fact any biological significance? Are the barred birds, by virtue of the possession of this color pattern, at any advantage in the struggle for existence? Is their relative inconspicuousness any real protection against their natural enemies? It is the purpose of this section of the paper to present some numerical data regarding this matter.

The only evidence which exists in the literature on this problem, so far as poultry is concerned, consists in the admittedly fragmentary statistics presented by Davenport, which have been cited above. It should be pointed

FIG. 4. A pure Barred Plymouth Rock ♀, with barring of fine quality from the fancier's standpoint. It is to be noted that the bird in this figure is in the shadow of a building in contrast to that shown in Fig. 3, which is standing in the bright sun.

out that Davenport's data are fragmentary not alone in respect to the small number of deaths (eliminations in the technical sense) involved, but also because these deaths were due to but a single one of the natural enemies of poultry, namely the crow. There are, of course, many others. Under the conditions prevailing on or about the poultry plant of which the writer has charge the following animals are regular or occasional destroyers of young chicks: Rats, skunks, foxes, crows, hawks, cats.[3]

In different seasons the relative importance of these different enemies varies. Thus in the breeding season of 1908 many birds were killed by foxes. In 1909, the year

[3] To this list one feels tempted to add that species of vermin which is in some respects the worst which attacks a poultry plant, namely the thief, but fortunately the *range* was free from his depredations in 1909.

for which statistics are given below, not a single bird was killed by a fox so far as is known. Similarly in 1909 no birds were killed by skunks. In 1910 a skunk succeeded in getting into a house one night and killed a number of birds. On the Maine Station plant normally predaceous birds undoubtedly rank first in destructiveness. This is probably quite generally true of poultry plants, though because of the fact that the loss is distributed so evenly over the whole season the importance of this class of enemies is apt to be underrated. Next to predaceous birds stand rats, under our conditions. An important point to be noted is that on the plant under discussion here all killing of chickens by rats is done in the daytime. Rats burrow in the ground under the houses, and then when the chicks are playing about a rat will dash out, seize a chick and carry it back to the burrow. It is not an uncommon occurrence for a rat thus to kill as many as 12 chickens within the space of an hour. With rare exceptions we never lose any chickens at night except those taken by thieves. The chicks are shut and locked in rat and (usually) vermin proof houses at night. Occasionally, as noted above, a skunk is able to effect entrance into a house. This, however, did not happen in 1909, the year which furnished the statistics given below. It should be clearly understood that in the statistics which follow all "eliminations" occurred in the daytime, when color and pattern might presumably be of some significance.

It is my purpose to present some statistics, involving a relatively large number of individuals, regarding the relation of color pattern to the elimination of chickens by all of these natural enemies taken together. These statistics cover the hatching season of 1909 in which chickens were on the range, and subject to the attacks of enemies, from about April 1 to October 1. Birds of all colors and patterns ran together on the same open, turf-covered range, and, without regard to color or pattern, all were equally exposed to attack by all sorts of

natural enemies. The total number of chickens involved was 3,343. An account of the way in which the statistics were obtained is necessary. All of these 3,343 chicks were of known pedigree, and a numbered aluminum leg band was attached to each one when it was removed from the incubator in which it was hatched. A record was made of each chick's number. This numbered leg band was worn by the chick throughout its life. Whenever a chick died a record of this fact was made opposite its entry in the pedigree book. During the season every living chick on the range was handled over twice and its leg band number checked back with the original entry, and at the end of the season all chicks remaining on the range were checked up.

Now it is clear that dead chicks which come to autopsy will fall into two general classes: on the one hand, those that died from one or another of the many *diseases* which make the poultry raiser's life a burden in the springtime, and on the other hand, those *killed by some enemy but not carried away*. In the latter class will fall the great majority killed by rats, some killed by skunks, and a fair proportion of those killed by foxes. Usually a direct record can be obtained for practically none of the chicks killed by predaceous birds and cats. In 1909 we have reason to believe that substantially all unrecorded deaths were caused by predaceous birds.

At the end of the season when the birds are checked up all will be accounted for as either (*a*) living, (*b*) dead from some disease, (*c*) killed by recorded enemies, or finally (*d*) missing. Of the missing birds there are two classes again. On the one hand are those killed by enemies which carried the carcases away, and on the other hand, are those that through accident lost their leg bands, and hence, while present in the flock, can not be entered upon the records. With the methods of work in use here the number of the latter class has always been small. Unfortunately I am not able to give exact figures for such birds for the season of 1909. It can be stated with cer-

tainty, however, that they did not exceed 25. Of this number that lost their leg bands 8 were known to be self-colored birds.

There were on the range in 1909 three classes of birds, in respect to color pattern. These were (*a*) barred birds, bearing either the pattern of the pure Barred Plymouth Rock, or a modification of it;[4] (*b*) solid (self-colored) black birds, resulting from the cross Cornish Indian Game ♂ × Barred Rock ♀; and (*c*) pure Cornish Indian Games of the dark variety which may for present purposes be classed as self-colored birds.

With this somewhat lengthy explanation of the composition of the flock and method of keeping records in hand we may proceed to examine the statistics of elimination. In compiling these statistics the blank birds which lost their bands (ca. 25) have been included with the eliminated. This does not affect the conclusions in any way because of the facts that (1) the number of such birds is so small relatively, and (2) the proportion of self-colored to barred birds among those which lost their bands is relatively higher than in the general population from which they came. The significance of this point will be apparent as we proceed.

We have the following figures, it being understood that "eliminated" means "killed by natural enemies" with the inclusion of the small number of birds which lost their bands as noted above.

Total number of birds = 3,343.
Number of *barred* birds = 3,007.
Number of *self-colored* birds = 336.
Total number of eliminated birds = 325.
Number of *barred* birds eliminated = 290.
Number of *self-colored* birds eliminated = 35.

The above figures include *all* eliminated birds, those killed by recorded and unrecorded enemies together. If we take only those killed by recorded enemies, which

[4] See Pearl, R., and Surface, F. M., "On the Inheritance of the Barred Color Pattern in Poultry," *Arch. f. Entwicklungsmech.*, Bd. XXX, Fest-Band für Roux), pp. 45–61, 1910.

under the conditions prevailing on the plant in 1909 means practically those killed by rats, we have:

Number of *barred* birds eliminated by recorded enemies = 68.

Number of *self-colored* birds eliminated by recorded enemies = 6.

From these figures the following proportions are derived: Of the *total number* of birds 10.05 per cent. were *self-colored.*

Of all the *eliminated* birds 10.77 per cent. were *self-colored.*

If we consider by themselves the birds eliminated by recorded enemies, we have:

Of the birds *eliminated by recorded enemies* 8.11 per cent. were self-colored.

Putting the figures in another way we have:

Of the *self-colored* birds 10.42 per cent. were eliminated by *all* enemies.

Of the *barred* birds 9.64 per cent. were eliminated by *all* enemies.

Of the *self-colored* birds 1.79 per cent. were eliminated by *recorded* enemies (chiefly rats).

Of the *barred* birds 2.26 per cent. were eliminated by *recorded* enemies.

Of the *self-colored* birds 8.63 per cent. were eliminated by *unrecorded* enemies (chiefly predaceous birds).

Of the *barred* birds 7.38 per cent. were eliminated by *unrecorded* enemies (chiefly predaceous birds).

The conclusion to be drawn from these figures, which involve a large number of individuals, is obvious. It is that *the relative inconspicuousness of the barred color pattern afforded its possessors no great or striking protection against elimination by natural enemies, during the season (April 1 to October 1) of 1909 on the poultry range of the Maine Experimental Station.* It might be objected that if the eliminations by predaceous birds alone could be separately recorded it would then be found that against this class of enemies the barred pattern had

great protective value, as suggested by Davenport's figures. This, however, can hardly be the case in the present statistics since if it be assumed that predaceous birds killed relatively few barred chicks and relatively many self-colored, then it must also be assumed that the other unrecorded enemies showed a *preference* for barred birds, since with all enemies taken together substantially equal proportions of both kinds of birds were eliminated. In other words, if we assume a selective elimination in the case of predaceous birds, we are obliged to assume an *equal* and *opposite* selective elimination on the part of other unrecorded enemies. There is no evidence on which such an assumption could be based.

These figures, of course, cover only one year's experience, and are in no wise conclusive, but general observation indicates strongly that essentially the same result would be shown in other years if it were possible to tabulate the figures. Unfortunately neither the records of 1908 nor 1910 can be used for this purpose. In 1908 there were almost no self-colored birds on the range. In 1910, owing to the location of the houses on the range and other circumstances which can not be gone into in detail, thieves were active on the plant and the birds taken were not a random sample of the flock in respect to color. 1909 was a fortunate year for such a study as the present one. The thieves confined their attention to adult stock on a part of the plant away from the chicks, and left the latter strictly alone.

Definitely controlled observations regarding the elimination of animals by natural enemies, covering a considerable number of individuals and anything like a complete range of enemies, are exceedingly scarce. The whole question of the interplay of factors in the "struggle for existence" constantly going on in the organic world has been discussed very largely from the *a priori* standpoint, throughout the whole period since the appearance of the "Origin of Species." The "rabbit with his legs a little longer," the "fox with the little keener

sense of smell," the "bird of dull colors which harmonized with the background," *et id genus omne*, have been made to do valiant service.

Ever since the first description, made by the Nuremberg miniature painter Rösel in 1746,[5] of a case of presumably protective coloration, we have been prone to argue that because an organism was colored or formed in such a way as to be inconspicuous it was, therefore, necessarily *protected* from attack by its enemies to a greater or less degree. The logic of such reasoning is flawless. It *ought* to be protected. But a conclusion may be perfectly logical and still not true. In the study of protective coloration, including mimicry, it is essential that a discovery that an organism is to human eyes inconspicuous or not readily distinguishable from some other organism shall not be considered the final goal. Rather let such a discovery always be supplemented by an experimental or observational determination of whether this inconspicuousness really helps the organism, in actual practise, in avoiding elimination by natural enemies. It is worth noting that more than one recent critical student of these problems who has applied this method has brought to light results essentially similar in their general import to those set forth here.[6]

[5] Cf. Müller, H., "Schützende Aehnlichkeit einheimischer Insekten," *Kosmos*, Jahrg. III, Heft 8, p. 114, 1879.

[6] Cf. for example the chapter on "Colouration of Organisms" in Dewar and Finn's "The Making of Species" (New York, 1909), and still more recently the thorough critical study by Punnett on "Mimicry in Ceylon Butterflies, with a Suggestion as to the Nature of Polymorphism" (*Spolia Zeylonica*, Vol. VII, Part XXV, September, 1910, pp. 1–24, 2 plates).

SOME CONSIDERATIONS CONCERNING THE PHOTOGENIC FUNCTION IN MARINE ORGANISMS

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IN two very interesting papers, Professor C. C. Nutting[1] has brought forth evidence tending to show that in oceanic depths below the range of penetration of the sun's rays, there exists a dim, phosphorescent light, quite general in its distribution, radiated from various photogenic organisms of the abyssal regions, and having a definite and valuable significance for the life of animal forms at these depths.

That such a light actually exists is scarcely to be sanely doubted, in view of the evidence of the deep-sea explorations which have added so much to the knowledge of oceanic conditions. And that it has a purpose in the life of the forms inhabiting those portions of the ocean beds where it exists, seems to the writer equally undeniable, unless we accept Emerson's poetic reasoning that

> "Beauty is its own excuse for being."

Just what its purpose may be in hermaphroditic, simple forms not provided with definite organs of sight, and indeed also in many higher forms, may, of course, still be a legitimate subject for investigation and consideration.

Professor Nutting's remarks have been of special interest to the writer in connection with some recent studies made by the latter on the general subject of biophotogenesis, with special reference to the Lampyridæ.[2]

[1] (*a*) "The Utility of Phosphorescence in Deep-sea Animals," AMER. NAT., Vol. 3, 1899, pp. 792–799; (*b*) "The Theory of Abyssal Light," *Proc. VII Cong. Zool.*, advance reprint, 1910.

[2] *Amer. Journ. Physiol.*, 1910 Vol. 27, pp. 122–151; *Canad. Entomol.*, 1910, Vol. 42, pp. 357–363; *Popular Sci. Monthly*, 1910, Vol. 77, pp. 114–121.

The coloring and photogenicity of the organisms found in the depths of the sea show some similarities to the corresponding features of life on land.

Take the family Buprestidæ, of the genus Coleoptera, of the order of insects. The insects of this family are probably the most brilliantly colored of any of the beetles, and are colored quite as brilliantly as the insects of any other genus. The colors cover a quite wide range of metallic, polished, glistening greens, blues, reds, coppery and golden; many of the smaller species wear more somber dark blues, browns and blacks, but as a class they are brilliant and showy. Obviously, these colors would be invisible in the absence of light, and need a light of considerable intensity to bring out their full value. Now we find that almost without exception these Coleoptera are diurnal; they attain their maximum activity during the brightest daylight, and fly but little at night. But one species has been reported to be luminous, and unless this report is pretty definitely confirmed there is grave reason to doubt its authenticity.

Now let us consider the Lampyridæ: The beetles of this family of almost eleven hundred species are in the great majority of instances, luminous; the non-luminous species form a decided minority of the true Lampyridæ. They are also, in the great majority of cases, mainly nocturnal in habit, hiding out of the sunlight during the day; those species which are markedly diurnal in habit are also those which are non-luminous, or in which the luminosity is relatively slight. In coloration, they show none of the bright metallic, showy colors of the Buprestidæ; black, gray, brown and yellow-brown predominate, with occasional red markings, yellow stripes and indistinct lines and spots. In them, the photogenic function possesses at least two definite significances: (1) it is an adjunct of the sexual organism of the insect, rendered of value to them by reason of their nocturnal habits, and (2) it has a protective value. In the larvæ it might also be considered to have an aggressive value, in attracting the snails, etc.,

on which they feed, but this argument would not hold for the imagos, which are much more active.

Most of the above statements apply with equal force to the Pyrophorini, the luminous Elateridæ of the tropics; these insects are herbivorous, however, and the aggressive significance does not hold for them.

It would seem, then, very probable that similar conditions obtain in the abyssal region, with its dim weird, phosphorescent light. The light produced by the Lampyridæ has recently been shown by Ives and Coblentz[3] to have the extremely high radiant efficiency of 96.5 per cent., against 4 per cent. for the best artificial illuminant. The spectrum of this light is a continuous band extending from the upper red to the lower blue with a maximum intensity in the yellow-green. This spectrum is of wider range than that of the sea-forms cited by Nutting,[4] but can hardly be of less efficiency. The light of the Lampyridæ is generally stated to be yellow, or greenish; there are some slight variations among different species, but in the main the lights are similar; it seems that a great many of the marine organisms also give a light of similar tone. Therefore colors whose wave-lengths are within the limits of those of the emitted lights of these forms, would be distinguishable in such a biophotogenic light. Although we do not yet know the full details of the process of the production of light by living forms, it is not too much to assume that Nature has developed it to a point very near to the maximum possible efficiency, and if such is the case, the luminous oceanic forms could emit a very penetrating illuminating radiation with very little expenditure of energy, and though this light might not be of any considerable intensity, as judged by our eyes, it could undoubtedly serve as quite a useful light to the large-eyed denizens of the deep.

The photogenicity of *Salpa*, *Noctiluca* and other such simple forms, which are without definite organs of sight,

[3] Bulletin of the U. S. Bureau of Standards, 1910, Vol. 6, pp. 321–336.

[4] *Supra b*, page 10.

presents other difficulties. It is not, however, necessary to the faculty of perception of light that definite organs should exist. It is a quite well-known fact that certain worms, bacteria, and other low organisms are able to detect ultra-violet rays to which the human organism is wholly without sensible response, and yet these actinotropic (if a coined word may be pardoned) forms show no definite organs such as might be adapted to the receiving and recording of the very short wave-lengths of ultra-violet light. If, then, existing organisms are known to be affected by ultra-violet rays for which they have no special sense-organs, it is certainly logical to assume that they and other forms may also be susceptible to the longer and more easily discerned wave-lengths of visible light—especially when those wave-lengths comprise mainly the rays possessing the highest illuminating effect—and without the necessity for the existence of "eyes" or other definite light-receiving organs. As a matter of fact *Noctiluca*, and numerous other marine organisms have been shown to be susceptible to light, although they possess no specific organs for this function so far as we have been able to make out.

Another consideration as to the purpose of the light presents itself here. We must consider the nature of the medium in which these creatures live. Water does not lend itself as readily as does air to the diffusion of the particles which produce the sensation of smell; and hence while odors, or speaking more properly, from the standpoint of marine organisms, flavors or tastes undoubtedly exist in the ocean water, they could not, on account of the water currents, lack of diffusion, etc., serve the purpose which the odors of land animals serve of giving indication of the presence and location of the creatures. It therefore would not be unreasonable to assume that in the gregarious simple luminous marine forms, the photogenic function takes the place to some extent of the animal odors of land forms.

To sum up, then:

From analogy to terrestrial forms, the photogenicity and coloration of marine organisms must play some essential part in their life histories;

The absence of definite organs for the reception of the radiations of light may not necessarily indicate that the forms from which they are absent are insensible to these radiations;

The photogenic function in certain simple marine forms may replace the olfactory function of terrestrial forms, to some extent.

SHORTER ARTICLES AND DISCUSSION

COMPUTING CORRELATION IN CASES WHERE SYMMETRICAL TABLES ARE COMMONLY USED

In studying the assortative mating of *Paramecium* I have found occasion to compute the correlation in many cases for which double or symmetrical tables are commonly employed. I have found that in such cases the use of symmetrical tables is quite unnecessary and the computations can be performed with much less labor without them. It will, therefore, be worth while to show how the use of symmetrical tables can be avoided.

When the two objects to be compared are alike, as when the two members, A and B, of conjugating pairs are examined, evidently either A or B might be entered in either the horizontal rows or the vertical columns of the correlation table. In such cases, the mean computed from the rows, and that computed from the columns are likely to differ, depending on which individuals were entered in the rows, which in the columns. If, for example, the larger individual is always entered in the vertical columns, the smaller in the horizontal rows, as in Table II, then the means and standard deviations of the two sets will differ much. As a result the coefficient of correlation computed in the usual way will show varying values, depending on how the pairs are entered in the table. From the collection shown in Table II we can by varying the method of entering the pairs get coefficients of correlation varying from 0.132 to 0.523.

Under such conditions Pearson (1901), Pearl (1907) and others enter each pair twice, once in the rows, once in the columns. This gives a "symmetrical" table, in which the sums of either the rows or the columns include all the individuals. This method is theoretically correct, since each individual functions both as "principal" and as "mate"; the coefficient of correlation computed from such symmetrical tables is the correct one. But such symmetrical tables are cumbersome and involve much labor. Pearl (1907) gives a formula by which the same coefficient can be obtained without making symmetrical tables, by computations involving the two means and standard

deviations and the coefficient of correlation found in the usual way.

But it is possible to find the correct coefficient of correlation from ordinary tables, and with much less labor than by either the use of symmetrical tables or by the method given by Pearl. To see how this can be done, it is well to examine a symmetrical table prepared for computation of the coefficient of correlation, such as is given in Table I. Here the large figures give the frequencies, while the subscripts in smaller type give the products of the deviations from the approximate mean (37). There are two main points to be considered: (1) How the quantity

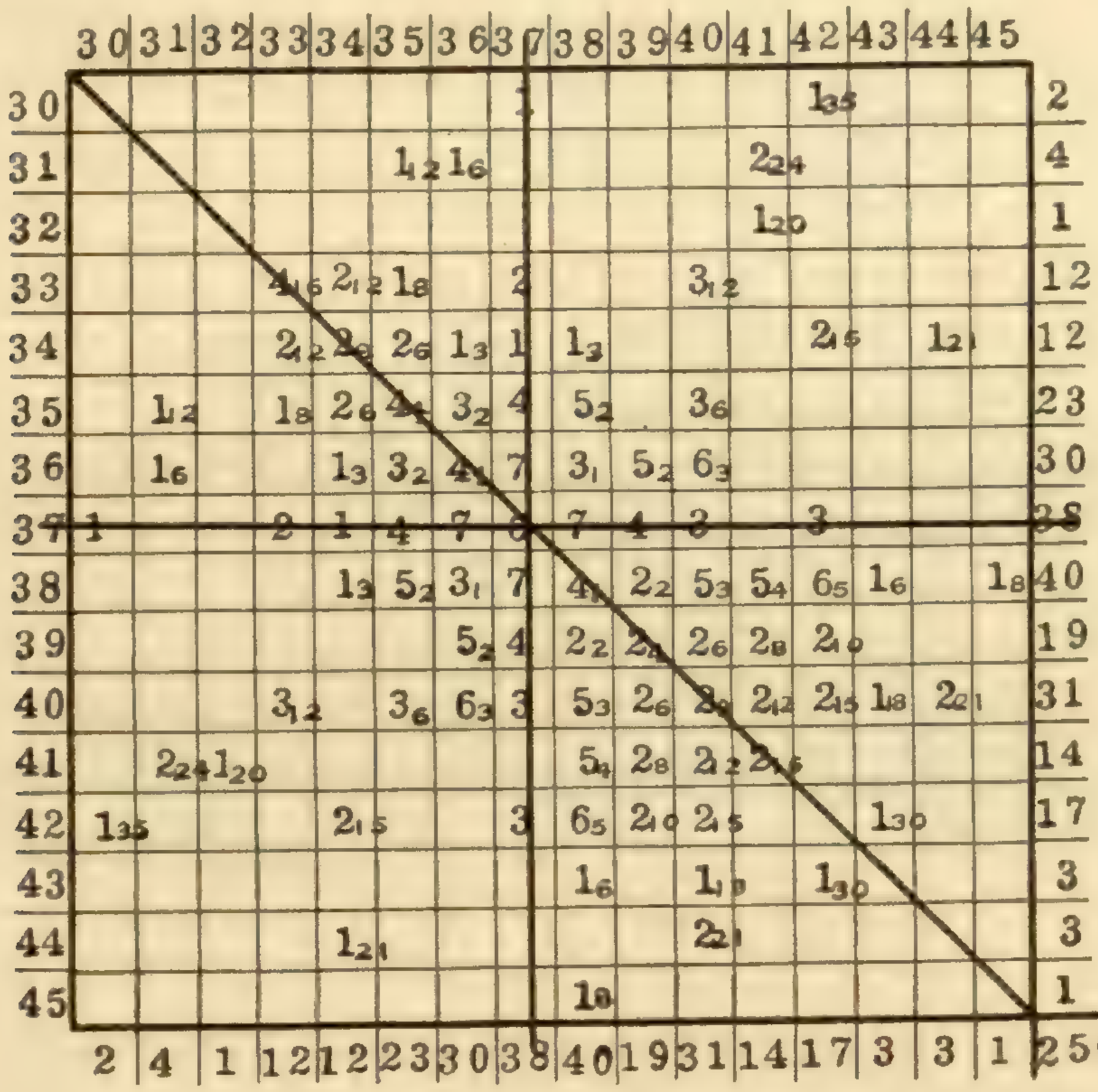

TABLE I. SYMMETRICAL CORRELATION TABLE FOR THE LENGTHS OF 125 PAIRS OF *Paramecium aurelia;* each individual entered twice, once in the vertical columns, once in the horizontal rows. (Unit of measurement, 4 microns.)

$S(xy)$ is to be correctly obtained; (2) how the mean and standard deviation are to be correctly obtained.

1. With regard to the first point, it will be observed that such a table is divisible by a diagonal passing from the upper left-hand corner to the lower right-hand corner into two halves which are in all respects duplicates as regards both frequencies and deviation products. (The frequencies through which the diagonal line passes are to be divided evenly between the two halves.) It is evident, therefore, that if we use only one of these halves

of the table in getting the sum $S(xy)$ we shall get just one half the sum we should get by using the whole table; the sum for the whole table would therefore be obtained simply by doubling this half-sum. Now, if in place of making a symmetrical table we enter always the larger member of each pair in the vertical columns, the smaller in the horizontal rows, we shall get a table that is precisely one of these duplicate halves of the symmetrical table; this will be seen by comparing Tables I and II. The quantity $S(xy)$ from such a table will then be just half that from the symmetrical table; it may then be doubled, and the further computation will be identical with that for the symmet-

	30₇	31₆	32₅	33₄	34₃	35₂	36₁	37	38₁	39₂	40₃	41₄	42₅	43₆	44₇	45₈	A	B′	C
30₇								1					1_{33}				2		2
31₆						1_{12}	1_6					2_{24}					4		4
32₅												1_{20}					1		1
33₄				2_{16}	2_{12}	1_8		2			3_{12}						10	2	12
34₃					1_9	2_6	1_3	1	1_3				2_{15}		1_{21}		9	3	12
35₂						2_4	3_2	4	5_2		3_6						17	6	23
36₁		Y					2_1	7	3_1	5_2	6_3						23	7	30
~~37~~								7	7	4	3		3				~~20~~	~~18~~	~~38~~
38₁									2_1	2_2	5_3	5_4	6_5	1_6		1_8	22	18	40
39₂										1_4	2_6	2_8	2_{10}				7	12	19
40₃											1_9	2_{12}	2_{15}	1_{18}	2_{21}		8	23	31
41₄												1_{16}					1	13	14
42₅														1_{30}			1	16	17
43₆																		3	3
44₇					X													3	3
45₈																		1	1
B			2	3	6	7	18		18	12	23	13	16	3	3	1	125	125	250

TABLE II. THE SAME TABLE SHOWN IN TABLE I, SAVE THAT EACH INDIVIDUAL IS ENTERED BUT ONCE—the larger member of the pair in the vertical column, the smaller in the horizontal row.

rical tables. Or (as we shall see) this half sum, which forms the dividend in obtaining the coefficient of correlation, may be divided by a number half as great as in the symmetrical tables, giving the same result.

It will further be seen that if in place of entering all pairs in the same way—the larger members in the columns, the smaller in the rows—we enter some or all of them differently, this will make no difference in the result. If in Table II, for example, the pair showing measurements 44 by 34 were entered in the reverse way, it would fall, no longer in the right upper quad-

rant, but in the left lower quadrant, at the point marked X. Here, as examination will show, it would receive the same subscript that it has now, and would count as negative, exactly as it now does. Again, suppose the pair 36 by 31 were similarly transposed; it would still fall in the left upper quadrant, at the point marked Y, where it would receive the same subscript as at present and count as positive, just as at present. And so of all other cases; the value of a pair is not altered in any way by changes in the way it is entered in the table. In making the table, therefore, the pairs may be entered only once and quite at random, or in any way that is convenient.

2. With regard to the mean and standard deviation, the apparent advantage of symmetrical tables is that they give us the actual mean of all the individuals; it is to this mean that our correlation must refer. But this actual mean can readily be obtained from the tables in which each pair is entered but once, in any way that happens to be convenient. It is merely necessary to add together the sums of the rows and of the columns of the table. Thus in Table II the number of individuals having the length 35 is not 17 (sum from the row beginning with 35), nor 6 (sum from the column headed 35), but 23 (sum from both the row and the column) and so for all other classes. It will be well to illustrate by an example certain of the steps in the computation. Table II shows a correlation table of single entry, as prepared for computation of the coefficients of correlation and other constants.

After finding the sums of the rows (given in column A at the right) and of the columns (given in B, underneath), we place the latter sums (B) by the side of A, in the proper places (as at B′), then add the two sets, giving the sums shown in the column C at the right. These are the same sums that we should get from a symmetrical table; adding these we get the total number of individuals (250 in Table II). Now from this column C we find the approximate mean in the usual way; it lies in this case at the length 37 (with 38 individuals). Through the column and the row headed 37 we therefore draw the lines serving as axes of reference in finding the correlation. We now find the correlation in the usual way. In so doing (1) we make use always of the sums in the column C in finding mean, standard deviation, etc. (2) We use for both horizontal and vertical axes of reference in computing the correlation in all cases

a row and column with the same heading (37 in this case). (3) We employ the ordinary frequencies in the body of the table in getting the sum of the deviations of (xy) for use in the formula for the coefficient of correlation, just as in ordinary correlation tables. The computation of the coefficient is of course (as in the case of symmetrical tables) considerably simpler than in the usual case, since we have but one standard deviation and one quantity d to deal with.

Only one other point in the computation is peculiar, requiring careful observance. If we let n signify the number of pairs and N the number of individuals (so that $N = 2n$), then in finding the mean, standard deviation, and coefficient of variation, we use N (just as in symmetrical tables), so that the formula for the standard deviation is

$$\sigma = \sqrt{\frac{S(x^2)}{N} - d^2} - .083.$$

But in getting the coefficient of correlation, the sum $S(xy)$ which we get from our unsymmetrical table is just half what we should get from a symmetrical table (as we have already seen). Therefore, to make the computations identical with those for symmetrical tables, we must either double this sum in the formula for the coefficient of correlation, or what is simpler, in place of doubling this sum we may halve the number by which we divide this sum, that is, we may use n in place of N. Thus the formula for the coefficient of correlation becomes by this method

$$r = \left(\frac{S(xy)}{n} - d^2\right) \times \frac{1}{\sigma^2}.$$

This method lends itself readily to the valuable procedure recently described by Harris (1910) for finding the coefficient of correlation, the only point requiring careful attention being the fact that in finding the standard deviation we must use N (number of individuals), while in the formula for the coefficient of correlation we must use n (number of pairs). The present plan is likewise well adapted for finding the coefficient of correlation by the "difference method" (see Harris, 1909).

If the method we have described is used, the pairs are entered in the table but once, in any way that is convenient; the correlation computed will always be the same, and identical with that from symmetrical tables. It avoids the cumbersome and labo-

rious symmetrical table; at the same time it involves much less labor than the method given by Pearl. When there are many tables to be computed, the amount of drudgery it saves is great.

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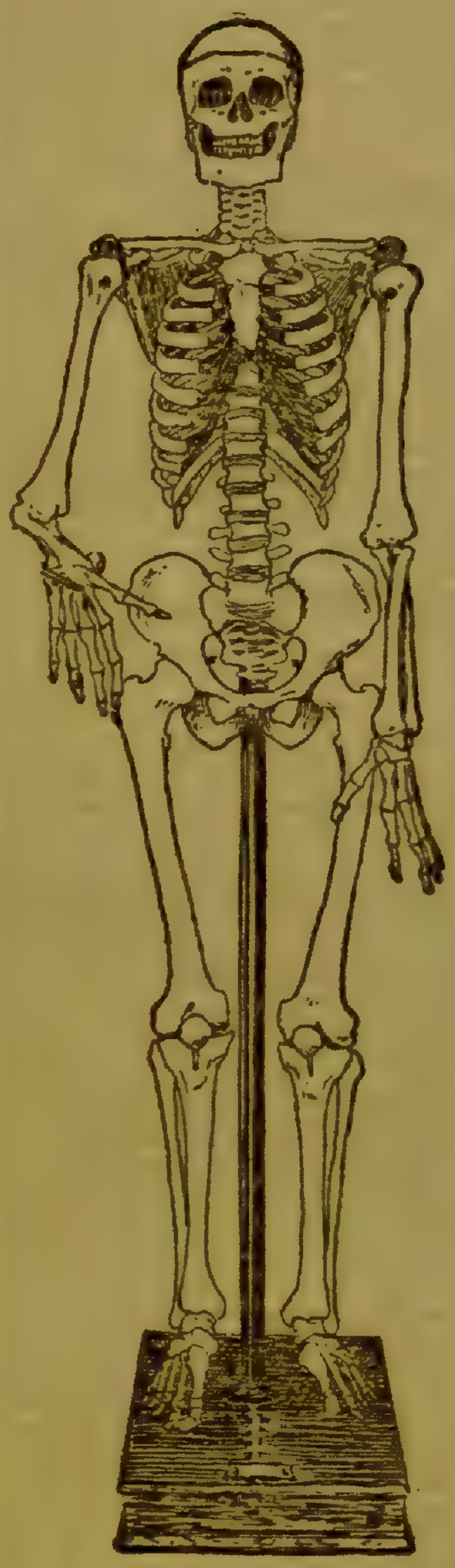

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Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

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The American Naturalist

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THE
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THE GENOTYPE CONCEPTION OF HEREDITY[1]

PROFESSOR W. JOHANNSEN
UNIVERSITY OF COPENHAGEN

BIOLOGY has evidently borrowed the terms "heredity" and "inheritance" from every-day language, in which the meaning of these words is the "*transmission*" of money or things, rights or duties—or even ideas and knowledge—from one person to another or to some others: the "heirs" or "inheritors."

The *transmission* of properties—these may be things owned or peculiar qualities—from parents to their children, or from more or less remote ancestors to their descendants, has been regarded as the essential point in the discussion of heredity, in biology as in jurisprudence. Here we have nothing to do with the latter; as to biology, the students of this science have again and again tried to conceive or "explain" the presumed *transmission* of general or peculiar characters and qualities "inherited" from parents or more remote ancestors. The view of natural inheritance as realized by an act of transmission, viz., the transmission of the parent's (or ancestor's) *personal qualities* to the progeny, is the most naïve and oldest conception of heredity. We find it clearly developed by Hippocrates, who suggested that the different parts of the body may produce substances which join in the sexual organs, where reproductive matter is formed.

[1] Address before the American Society of Naturalists, December, 1910.

Darwin's hypothesis of "pangenesis" is in this point very consistent with the Hippocratic view, the *personal* qualities of the parent or the ancestor in question being the heritage.

Also the Lamarckian view as to the heredity of "acquired characters" is in accordance with those old conceptions. The current popular definition of heredity as a certain degree of resemblance between parents and offspring, or, generally speaking, between ancestors and descendants, bears the stamp of the same conceptions, and so do the modern "biometrical" definitions of heredity, *e. g.*, as "the degree of correlation between the abmodality of parent and offspring." In all these cases we meet with the conception that the personal qualities of any individual organism are the true heritable elements or traits!

This may be characterized as the "transmission-conception" of heredity or as the view of *apparent* heredity. Only superficial instruction can be gained by working on this basis. Certainly, medical and biological statisticians have in modern times been able to make elaborate statements of great interest for insurance purposes, for the "eugenics-movement" and so on. But no profound insight into the biological problem of heredity can be gained on this basis, for the transmission-conception of heredity represents exactly the reverse of the real facts, just as the famous Stahlian theory of "phlogiston" was an expression diametrically opposite to the chemical reality. The *personal qualities* of any individual organism do not at all cause the qualities of its offspring; but the qualities of both ancestor and descendant are in quite the same manner determined by the nature of the "sexual substances"—*i. e.*, the gametes—from which they have developed. Personal qualities are then *the reactions of the gametes* joining to form a zygote; but the nature of the gametes is not determined by the personal qualities of the parents or ancestors in question. This is the modern view of heredity.

The main result of all true analytical experiments in questions concerning genetics is the upsetting of the transmission-conception of heredity, and the two different ways of genetic research: pure line breeding as well as hybridization after Mendel's model, have in that respect led to the same point of view, the "*genotype-conception*" as we may call the conception of heredity just now sketched.

Here we can not trace the historical evolution of the ideas concerning heredity, not even in the last ten years, but it must be stated as a fact that a very great number of the terms used by the modern biological writers have been created under the auspices of the transmission-conception, and that perhaps the greater number of botanists and zoologists are not yet emancipated from that old conception. Even convinced Mendelians may occasionally be caught using such words as "transmission" and other now obsolete terms.

The science of genetics is in a transition period, becoming an exact science just as the chemistry in the times of Lavoisier, who made the balance an indispensable implement in chemical research.

The "genotype-conception," as I have called the modern view of heredity, differs not only from the old "transmission-conception" as above mentioned, but it differs also from the related hypothetical views of Galton, Weismann and others, who with more or less effectiveness tried to expel the transmission-idea, having thus the great merit of breaking the ground for the setting in of more unprejudiced inquiries. Galton, in his admirable little paper of 1875, and Weismann, in his long series of fascinating but dialectic publications, have suggested that the elements responsible for inheritance (the elements of Galton's "stirp" or of Weismann's "Keimplasma") involve the *different organs* or tissue-groups of the individual developing from the zygote in question. And Weismann has furthermore built up an elaborate hypothesis of heredity, suggesting that discrete particles of

the chromosomes are "bearers" of special organizing functions in the mechanism of ontogenesis, a chromatin-particle in the nucleus of a gamete being in some way the representative of an organ or a group of tissues.

These two ideas: that "elements" in the zygote correspond to *special organs*, and that *discrete particles of the chromosomes* are "bearers" of special parts of the whole inheritance in question are neither corollaries of, nor premises for, the stirp- or genotype-conception. Those special ideas may have some interest as expressions of the searching mind, but they have no support in experience; the first of them is evidently erroneous, the second a purely speculative morphological view of heredity without any suggestive value.

The genotype-conception of the present day, initiated by Galton and Weismann, but now revised as an expression of the insight won by pure line breeding and Mendelism, is in the least possible degree a speculative conception. Of all the Weismannian armory of notions and categories it may use nothing. It is a well-established fact that language is not only our servant, when we wish to express—or even to conceal—our thoughts, but that it may also be our master, overpowering us by means of the notions attached to the current words. This fact is the reason why it is desirable to create a new terminology in all cases where new or revised conceptions are being developed. Old terms are mostly compromised by their application in antiquated or erroneous theories and systems, from which they carry splinters of inadequate ideas, not always harmless to the developing insight.

Therefore I have proposed the terms "gene" and "genotype" and some further terms, as "phenotype" and "biotype," to be used in the science of genetics. The "gene" is nothing but a very applicable little word, easily combined with others, and hence it may be useful as an expression for the "unit-factors," "elements" or "allelomorphs" in the gametes, demonstrated by modern Mendelian researches. A "genotype" is the sum total of

all the "genes" in a gamete or in a zygote. When a monohybrid is formed by cross fertilization, the "genotype" of this F_1-organism is heterozygotic in one single point and the "genotypes" of the two "genodifferent" gametes in question differ in one single point from each other.[2]

As to the nature of the "genes" it is as yet of no value to propose any hypothesis; but that the notion "gene" covers a reality is evident from Mendelism. The Mendelian workers have the great merit of being prudent in their speculations. In full accordance with this restraint —a quite natural reaction against the morphologico-phantastical speculations of the Weismann school—it may be emphatically recommended to use the adjectival term "genotypical" instead of the noun "genotype." We do not know a "genotype," but we are able to demonstrate "genotypical" differences or accordances. Used in these derivated ways the term "gene" and "genotype" will prejudice nothing. The very appropriate German term "Reaktionsnorm" used by Woltereck is, as may be seen, nearly synonymous with "genotype," in so far as the "Reaktionsnorm" is the sum total of the potentialities of the zygotes in question. That these potentialities are partly separable ("segregating" after hybridization) is adequately expressed by the "genotype" as composed of "genes." The "Reaktionsnorm" emphasizes the diversity and still the unity in the behavior of the individual organism; certainly, the particular organism is a whole, and its multiple varying reactions are determined by its "genotype" interfering with the totality of all incident factors, may it be external or internal. Thence the notion "Reaktionsnorm" is fully compatible with the genotype-conception.

The genotypes can be examined only by the qualities and reactions of the organisms in question. Supposing

[2] They may therefore be characterized as "mono-genodifferent"; this term and the further terms "di-genodifferent" and so on, may or may not be of any use.

that some organisms of identical genotypical constitution are developing under different external conditions, then these differences will produce more or less differences as to the personal qualities of the individual organisms. By simple inspection of series of different individuals it will be quite impossible to decide if they have or have not the same genotypical constitution—even if we know them to be homozygotic.[3] We may easily find out that the organisms in question resemble each other so much that they belong to the same "type" (in the current sense of this word), or we may in other cases state that they present a disparity so considerable that two or more different "types" may be discerned.

All "types" of organisms, distinguishable by direct inspection or only by finer methods of measuring or description, may be characterized as "*phenotypes.*" Certainly phenotypes are *real things;* the appearing (not only apparent) "types" or "sorts" of organisms are again and again the objects for scientific research. All typical phenomena in the organic world are *eo ipso* phenotypical, and the description of the myriads of phenotypes as to forms, structures, sizes, colors and other characters of the living organisms has been the chief aim of natural history, which was ever a science of essentially morphological-descriptive character.

Morphology, supported by the huge collections of the museums, has of course operated with phenotypes in its speculations concerning phylogenetic questions. The idea of *evolution by continuous transitions* from one "type" to another must have imposed itself upon zoologists and botanists, because the varying external conditions of life are often[4] shifting the phenotypes in very fine gradations; but also—and that is an important point—because there may always be found considerable genotypical differences hidden in *apparently homogeneous populations,* exhibiting only one single "type" around

[3] Here we are not concerned with the question of variable dominance, etc.

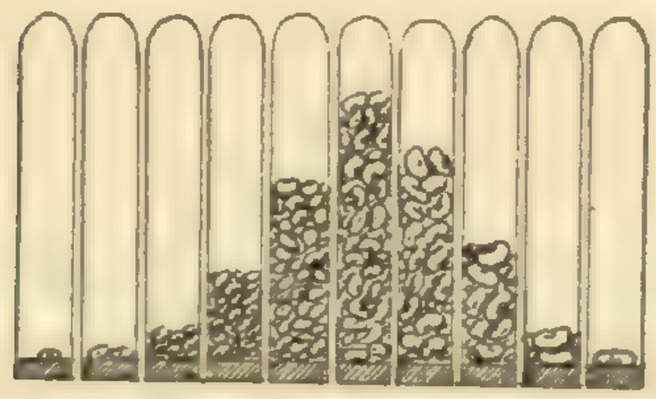
[4] Not always, as Bateson has the merit of having emphasized.

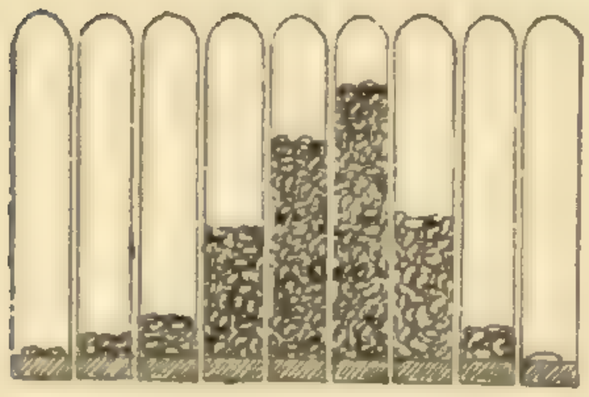
which the individuals fluctuate. For the descriptive-morphological view the manifestations of the phenotypes in different generations are the main point, and here the transmission-conception immediately announces itself. Hence we may adequately define this conception as a "phenotype-conception" in opposition to the genotype-conception.

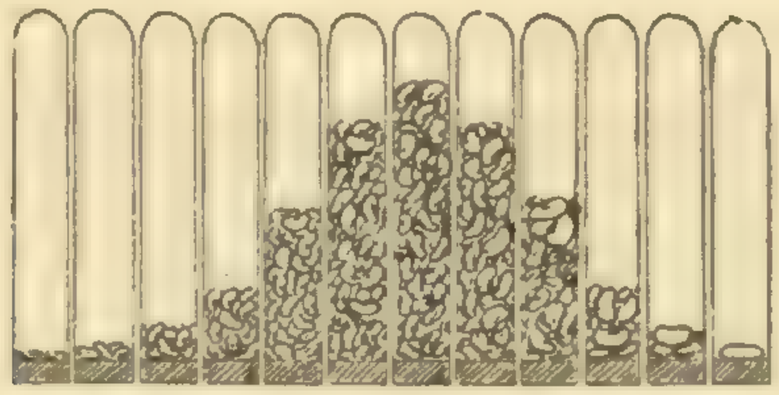
As already stated, the genotype-conception has been gained in two ways: pure line breeding and hybridization. The first way leads to an analysis of the existing stocks or populations, the second way may realize an analysis of the genotypical constitution of the individuals. The analysis of populations has its most obvious importance in all such cases, where the phenotypes are quantitatively characterized. Even where individuals with considerable genotypical differences co-exist, the population may —by simple inspection or by statistical appreciation—seem to exhibit only one phenotype, this being usually characterized by the average measure of the individuals (dimensions, weight, intensity of any quality, number of organs and so on). This is due to the fluctuating variability swamping all limits between the different special phenotypes in question (see the diagram).

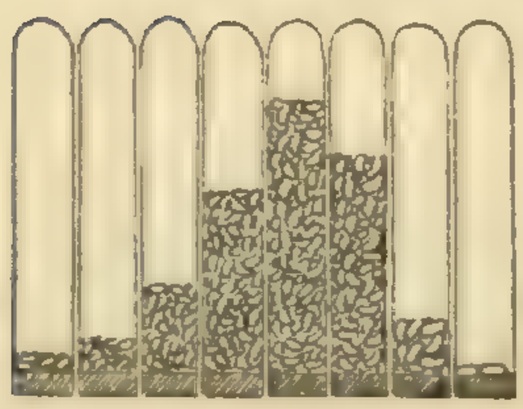
Populations of self-fertilizing organisms (several cereals and beans, peas and others) have offered the starting point for *pure line breeding* as a scientific *method of research*. A pure line may be defined as the descendants from one single homozygotic organism, exclusively propagating by self-fertilization. "Pure line" is a merely *genealogical term*, indicating nothing as to the qualities of the individuals in question. A "line" ceases to be "pure" when hybridization (or even intercrossing) disturbs the continuity of self-fertilization.

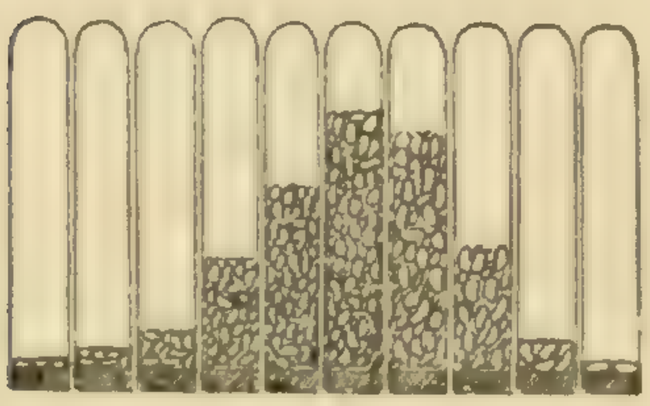
From a population of homozygotic self-fertilizers there can be started (isolated) as many pure lines as there are fertile individuals—of course very many of such pure lines will be quite identical in genotypical constitution and might in reality belong to one and the

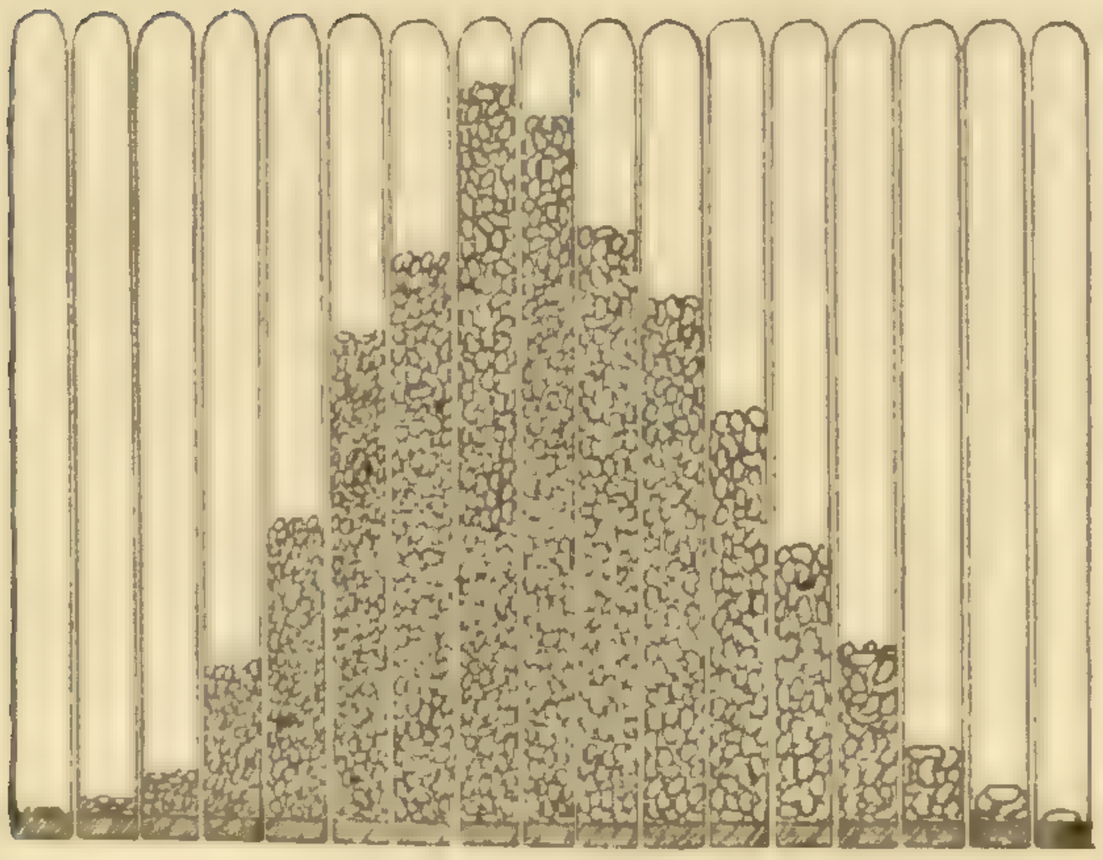












EXPLANATION OF DIAGRAMS

DIAGRAMS SHOWING FIVE DIFFERENT PURE LINES OF BEANS AND A "POPULATION" FORMED BY THEIR UNION. In each case the beans enclosed in glass-tubes are marshalled in equidistant classes of length; identical classes are superposed. The pure lines show transgressive fluctuation: it is mostly impossible to state by simple inspection of any individual bean the line to which it belongs.—The fluctuations about the average length (the phenotype) within the pure lines as well as in the mixed population show no characteristic difference.

same pure line if the genealogy was but sure. The guarantee of the descendence is thus a main point in the principle of pure lines. Identity of genotypical nature is not at all a proof for identical genealogy: the widespread confusion of "resemblance" with "genealogical relation" is the root of much evil—of which the statistics of biometricians have given us some instances.

The isolation of pure lines from plant-populations has been the instrument for gaining the conviction that *selection is not able to shift the nature of genotypes.* The well-known displacement of the "type" of a population by selection—this displacement proceeding from generation to generation in the direction indicated by the selection—is due to the existence *a priori* of genotypical differences in such populations (see the diagram). By selection a relatively great number of those organisms, whose genotypical constitution is favorable for the realization of the desired degrees of any character, will be saved for reproduction; hence the result of the selection!

Within pure lines—if no mutation or other disturbances have been at work—or within a population in which there is no genotypical difference as to the character in question, selection will have no hereditary influence. This result has in recent years also been reached by several other experimenters in genetics. Here I also may recall the brilliant experiments of H. S. Jennings with Paramœcium, experiments which have been carried out quite independently of my own researches and which have been of great importance for the propagation and support of the genotype-conception. The bearing

It can not be detected by inspection that the five upper diagrams represent phenotypes which are genotypically homogeneous, while the nethermost diagram —the sum of the others—indicates a phenotype masking five others. That these five phenotypes all are genotypically different is known *a priori* in this special case, but it could not be discerned by simple inspection.—In the population genotypical differences are combined with merely individual fluctuations; within the single pure line only such fluctuations are seen. Hence, while selection within a *pure line* will have no hereditary influence, it is evident that any selection in the *population* must shift or move the "type" of the progeny in the direction of selection.

of these experiments has been attacked on the ground that the Paramœciums multiply asexually; but this matter seems to me of no importance in the present case. The experience that pure-line breeding of plants and pure-strain cultures of micro-organisms, in full agreement, demonstrate the non-adequacy of selection as a genotype-shifting factor, is a circumstance of the greatest interest. Also Woltereck's experiments with Daphnias, the important researches of Wolff, and the highly interesting indications of C. O. Jensen as to bacteria may be mentioned here as further supports for this view. Quite recently Pearl has arrived at the same conclusion as to the egg-production by fowls.

The famous Galtonian law of regression and its corollaries elaborated by Pearson pretended to have established the laws of "ancestral influences" in mathematical terms. Now, by the pure-line explanation of the well known action of selection in poly-genotypic populations, these laws of correlation have been put in their right place; such interesting products of mathematical genius may be social statistics *in optima forma*, but they have nothing at all to do with genetics or general biology! Their premises are inadequate for insight into the nature of heredity.

Ancestral influence! As to heredity, it is a mystical expression for a fiction. The ancestral influences are the "ghosts" in genetics, but generally the belief in ghosts is still powerful. In pure lines no influence of the special ancestry can be traced; all series of progeny keep the genotype unchanged through long generations. A. D. Darbishire's laborious investigations as to the classical object of Mendel's researches, green and yellow peas, may even convince a biometrician that the ancestral influence is zero in "alternative inheritance." Ancestral influence in heredity is, plainly speaking, a term of the "transmission-conception" and nothing else. The characters of ancestors as well as of descendants are both in quite the same manner reactions of the geno-

typical constitution of the gametes in question. Particular resemblances between an ancestor and one or more of his descendants depend—so far as heredity is responsible—on corresponding particular identities in the genotypical constitution, and, as we have urged here, perhaps to excess, the genotype is not a function of the personal character of any ancestor.

The genotypic constitution of a gamete or a zygote may be parallelized with a complicated chemico-physical structure. This reacts exclusively *in consequence of its realized state,* but not in consequence of the history of its creation. So it may be with the genotypical constitution of gametes and zygotes: its history is without influence upon its reactions, which are determined exclusively by its actual nature.

The genotype-conception is thus an "ahistoric" view of the reactions of living beings—of course only as far as true heredity is concerned. This view is an analog to the chemical view, as already pointed out; chemical compounds have no compromising ante-act, H_2O is always H_2O, and reacts always in the same manner, whatsoever may be the "history" of its formation or the earlier states of its elements. I suggest that it is useful to emphasize this "radical" ahistoric genotype-conception of heredity in its strict antagonism to the transmission- or phenotype-view.

As to the evolution of human civilization we meet with *true ancestral influences,* viz., the *tradition* (comprising literature, monuments of art, etc., and all forms of teaching). Tradition is playing a very great rôle, but tradition is quite different from heredity. Nevertheless there may often be danger of confusion, and here the use of false analogs is not harmless. So an obscure metaphor is involved in archeologists' reference to Greek temples as "ancestors" of some types of Christian churches, or in their speaking of the descent of violins from more primitive "ancestors." Certainly, evolution of types of tools, instruments and implements of all kinds is—at least partially—going on by means of select-

ive factors combined with tradition, the latter not only conserving the valuable types but actively stimulating their improvement. But all this has nothing at all to do with the biological notion of heredity. It is of course interesting to see that the idea of "evolution by selection" has won credit in archeology, sociology, etc., but this involves nothing as to genetics, for which "tradition" is irrelevant.

The very "radical" form of the genotype-conception advocated here may be too "theoretical" to be carried through in all its consequences in cases of practical experiments in genetics. In nature and even in the chemical factories the chemical compounds are not always to be had in quite pure state. The history of a preparation may sometimes be traced by accompanying impurities. As to the analogy with the genotypes we touch here the question whether the genotypical constitution of a gamete may not be accompanied by some accessorial or accidental "impurities" from the individual organism in which the gamete was developed.

Here we meet with the cases of "spurious" heredity, *e. g.*, the infections of the gametes or zygotes as may be seen in certain cases of tuberculosis, syphilis, etc. Such and other forms of spurious heredity may have the appearance of "hereditary transmission" or "ancestral influence"; but theoretically they do not interfere at all with the genotype-conception of heredity. In such interesting cases as that detected by Correns, viz., the "heredity" of a special form of albinism by "transmission" through the plasm of the ovum—the sperm not transmitting this character—we may at the first glance be puzzled. Nevertheless, as Correns himself points out. here we have certainly to do with a pathological state of the plasm or the chromatophores in question, and that may perhaps be the reason for the lack of heredity through the sperm which carries no (?) plasm or only a small quantity. The etiology of such abnormalities being as yet quite unknown, it may often be very difficult to distinguish them clearly from "genotypically" de-

termined abnormalities which show the normal form of heredity through both ovum and sperm. The case quoted demands further experience and seems not to be in accord with results of Baur's experiments. At any rate, there may be several difficulties to overcome in the full and consistent application of the genotype-conception, difficulties that may be characterized as perturbations by infection or contamination. And hereby it must be remembered that theoretically, as well as practically, there are no sharp limits between "normal" and "pathological" manifestations of life. "Nature is beautiful, but not correct," is a Danish saying.

The principle of pure lines or, generally, pure culture, is of importance also for elucidating the celebrated question of the inheritance of "acquired characters." Mendelism and pure-line researches are here in the most beautiful accordance, both emphasizing the stability of genotypical constitution; the former operating with the *constituent unities*, the latter with the behavior of the *totality* of the genotypes in question. The brilliant work of Tower with Leptinotarsa and the highly suggestive injection experiments of MacDougal indicate that changes of the genotypical constitution are produced by steps, discontinuously. And as yet no experiment with genotypically homogeneous cultures has given any evidence for the Lamarckian view, the most extreme "transmission"-conception ever issued. As to bacteria, the important experiments recently made by C. O. Jensen for the purpose of changing their types through adaptation have given not only absolutely negative results, but have demonstrated the fallacy of some positive indications by previous authors. Lamarckism and selectionism are certainly at bottom the same thing: the belief in personal qualities being "transmitted" to the offspring. Observations in impure populations are now their places of resort; nevertheless, it is granted that their history in biology as suggestive ideas has been most glorious.

Apropos, some cases of apparent action of selection

may have direct touch with Lamarckian ideas, as, *e. g.*, De Vries's selection of buttercups, recently quoted by Jennings as "the only case that he has found" indicating hereditary action of selection: "Here, after selection the extreme was moved far beyond that before selection." And Jennings says: "Possibly repetition with thorough analytical experimentation will show that something besides selection has brought about the great change. But at present the case stands sharply against the generalizations from the pure line work."

Certainly Jennings is in reason, when he, on the ground of his own masterly researches, looks out for "something besides selection." There are three directions for the inquiry here. First, the strong evidence that the buttercup-population was not at all homogeneous. Secondly, the possibility of intercrossing. I only need to point out the beautiful researches of Shull as to the effect of intercrossing in maize. The heterozygotes were here larger and more productive than the pure strains. The surprises of heterozygotic "constructions" or of new combinations in F_2 may perhaps be responsible for the case of De Vries's buttercups; I shall not try to discuss it. But, thirdly, we have an instance pointed out several times by De Vries himself, viz., the *combination of selection with nourishment:* "la sélection c'est l'alimentation" as it has been said. I suppose that we have here the essential point. The buttercups in culture have been better nourished than before the experiments. Hence, the "best" genotypes having been selected from the population and submitted to "better" nourishment, the result would easily be a moving of the extremes far beyond those before selection. The buttercup-case seems to me to present no difficulties for the genotype-conception.

The practical breeders are a somewhat difficult people to discuss with. Their methods of selection combined with special training and "nurture" in the widest sense of this word are mostly unable to throw any light upon questions of genetics, and yet they only too frequently

make hypotheses as to the nature of heredity and variability. Darwin has somewhat exaggerated the scientific value of breeders' testimonies, as if a breeder *eo ipso* must be an expert in heredity. As to the principle of pure lines it has been occasionally vindicated by German authors, *e. g.*, K. v. Rümker, that pure line breeding is a thing old and well known. This is quite true; nearly sixty years ago L. Vilmorin not only emphasized in a lucid manner the importance of pure breeding, but he even tried a little to use his experiences theoretically. But it can not be denied that the principle of pure lines, as a true scientific analytical implement, as an indispensable *method of research in heredity*—not merely as a questionable and, at any rate, unilateral and insufficient method of practical breeding—is a novelty from recent years. Had this analytical principle been used in the times of Darwin, or had it even been appreciated in due time by the biometric school, certainly the real bearing of selection might long since have been rightly understood also by the practical breeders of pure strains.

The genotypes may then be characterized as something fixed and may be, to a certain degree, parallelized with the most complicated molecules of organic chemistry consisting of "nuclei" with a multitude of "side-chains." Continuing for a moment such a metaphor, we may even suggest that the genes may be looked upon as analogs of the "radicals" or "side-chains." All such ideas may as yet be premature; but they are highly favored by the recent researches of Miss Wheldale.

The fixity of a genotypical constitution in question is the conception arrived at by Mendelian and pure line work. Hence there is a *discontinuity* between different *genotypes*. This discontinuity has been energetically contested by several biologists, among whom Woltereck may be pointed out as an important representative. In his very interesting report on experiments with Daphnias, Woltereck indicates, as said above, that *selection was as yet ineffective;* moreover he describes *a case of discontinuous alteration* of type (mutation), and his ex-

periments designed to confirm the Lamarckian view have given as yet negative results, even though these may be called "promising," as he says. So all the evidence of his breeding experiments is in reality quite in favor of our genotype-conception!

But how much depends upon our mental eyesight, what we see. Woltereck confesses openly his belief in continuous evolution and remarks that for a convinced selectionist of the Weismann school the new genotype-conception is a "hard blow." The aim of his paper in question is to parry off such blows. Of course this parry can not use his own statements just mentioned; as to their obvious but inconvenient accordance with our conception Woltereck might apply the famous words from Harvey's times: "*video sed non credo.*" Hence the arguments must be taken from other observations, and some very instructive results of cultures under varying conditions have supplied the *pièce de résistance* for the discussion. Woltereck is within his right when asserting that we consider different genotypes as having *constant differences* (like different formulas in chemistry). This is an essential point; but Woltereck, admitting no constancy in the differences, tries to demonstrate that our view must be fallacious.

In a very suggestive manner he presents "phenotype-curves" for several pure strains. These curves are graphical schemes expressing (for the strain in question) the average degree or intensity of any particular character as it manifests itself under different conditions, *e. g.*, the relative length of heads by poor, intermediate and rich feeding, etc. Such "phenotype-curves" may indeed be very useful as records of the behavior of the organisms in question, and they mark certainly a valuable progress in descriptive methods.

The phenotype-curves of the Daphnias in question sometimes show rather constant differences between the pure strains compared; but mostly this is not the case. Especially under extreme conditions, *e. g.*, with poor or even with very rich feeding, some of the curves are con-

fluent. So the differences between the phenotype-curves may vary considerably or may even vanish entirely. These experiences agree with numerous observations of Wesenberg Lund as to the *Daphnias* in the Danish lakes, and there is no doubt as to their correctness.

But when Woltereck thinks that these facts are inconsistent with the existence of constant differences between the genotypes, he shows himself to have totally misunderstood the question! Of course the *phenotypes* of the special characters, *i. e.*, the *reactions of the genotypical constituents*, may under different conditions exhibit all possible forms of transition or transgression —this has nothing at all to do with constancy or inconstancy of genotypical differences.

Every student of genetics ought to know this; some few examples may suffice to enforce it: Temperature has great influence upon the intensity of color in flowers; all shades of intensity from saturated reddish-blue to pure white may be observed with different temperatures in lilac flowers of the "colored" varieties. Such pure white flowering individuals are—as to color—phenotypically not distinguishable from genotypically pure "white" varieties. Nobody will assume that there should be *genotypical* transitions here! Pure lines of beans may in one year be different in size, *e. g.*, the average of the line *A* exceeding that of *B*. In another year *B* may exceed *A*, or their average sizes may be practically identical. Differences of soil may produce something similar, and it is well known to breeders that some strains of wheat yield relatively much better than others on rich soil, while the reverse is realized on poorer soils. In four subsequent years two pure lines of barley, both characterized by a considerable degree of disposition to produce vacant spikelets (aborted grains) in the heads, presented the phenotypes here indicated in percentages of such vacancies.

Pure line *L*:	30	33	27	29
Pure line *G*:	5	45	3	28

The genotype-differences are nevertheless constant; the "Reaktionsnorms" of the organisms in Woltereck's cases, as well as in the examples just cited, are of course *eo ipso* "constantly different" just as well as the "Reaktionsnorms" of different chemical compounds. And as to chemical analogies it may perhaps be useful to state that different chemical compounds (the structural or constitutional differences of which surely are granted to be discontinuous and constant) may sometimes show "reaction-curves" highly resembling Woltereck's "phenotype-curves." It is, I suppose, quite sufficient to point out the temperature-curves of solubility for different salts of sodium and other metals. These curves interfere in different ways, cutting each other or partially confluent, in analogy with Woltereck's phenotype-curves.

The essential point in the whole matter is, of course, that a special genotypical constitution always reacts in the same manner under identical conditions—as all chemical or physical structures must do. Differences in genotypical constitution (as well as differences in chemical or physical nature) are not bound to manifest themselves at all—and still less to do so in the same sense—under all conditions. Sometimes even quite special conditions may be required for the realization of possibilities ("Potenzen," as some German authors are saying), due to a special genotypical nature: This is a well-known fact in physiology as in the fine art of gardening. Baur has long since emphasized the importance of this point for the Mendelian researches.

So the criticisms of Woltereck as to the genotypical discontinuity and constancy are only based upon a regrettable misconception of the genotype-notion. Over and over we find in current literature this confusion of genotypes with phenotypes, and we even have met with the idea, that the Daphnias of a lake may in summer diverge in different races or varieties, but that in winter they converge into one single race! In this statement of Wesenberg Lund, the author regards of course only the phenotypes in a purely descriptive manner. It is evident

that Woltereck's view has been influenced by Wesenberg Lund in this matter; but what might be fairly excused in the latter is not allowable for an experimenter pretending to work with cardinal questions of genetics.

Discontinuity and constant differences between the "genes" are the quotidian bread of Mendelism, and here the harmony of Mendelism and pure line work is perfect. We have dealt with some recent criticism of the pure line results; now it is time to look at Mendelism. The astonishing evolution of this mode of research has given an almost interminable stock of special results, and cases that at first might seem incompatible with the Mendelian views have been analyzed more thoroughly on a large scale and have shown themselves quite in accordance with Mendelism. The magnificent book of Bateson gives a full account of this prosperous state of Mendelian research. And it may be evident that Mendelism gives the most striking verification of the essential point in Galton's "stirp-hypothesis": the inadequacy of the personal quality in heredity. At the same time it overthrows totally the idea of "*organs*" as being represented by the unities of the "stirp," pointing out that the personal qualities of *the organism in toto* are the results of the reactions of the genotypical constitution. The segregation of one sort of "gene" may have influence upon the whole organization. Hence the talk of "genes for any particular character" ought to be omitted, even in cases where no danger of confusion seems to exist. So, as to the classical cases of peas, it is not correct to speak of the gene—or genes—for "yellow" in the cotyledons or for their "wrinkles,"—yellow color and wrinkled shape being only reactions of factors that may have many other effects in the pea-plants. It should be a principle of Mendelian workers to minimize the number of different genes as much as possible.

Here we meet with the questions of correlation and "coupling" of genes. I can not here enter into a discussion as to the notion of "correlation" with its several meanings; in my "Elemente der exakten Erblichkeits-

lehre'' a rather full discussion is to be found. I may only point out here that many cases of presumed correlation may simply be cases of two or more characters (reactions) due to the presence—or even absence—of one single gene. The phenotypically distinct and even diversely localized ''characters'' convey easily the impression that they are reactions of different genes.

The highly interesting experiences of Correns, Doncaster, Morgan, Spillman and others as to the sex-determining factors, are in some way connected with researches of correlation and ''coupling'' of genes. The discussion of the ingenious Bateson-Punnett scheme for *Abraxas* and Morgan's suggestive schemes as to Drosophila may favor the idea of what may be called ''ramified'' genes. Castle has in his splendid researches as to color-factors in rabbits, etc., initiated a systematic description of the (partially) analyzed genotypes, somewhat resembling the formulas of organic ''structural chemistry.'' If we suggest an analogy between the radicals of chemistry and the genes, the (partial) genotype-formulas in Castle's manner may be able to demonstrate ramifications of the genes inserted upon the main group of the genotype-constituents. Pausing a moment on this metaphor, it may be suggested that the ''branch.'' or ''branches'' of a ramified gene may be more difficult to separate from its ''trunk'' than the whole gene from the totality of the genotype. I shall here only ask if such views may be of any use as working hypotheses. Their bearing as to the realization of mutations is obvious,—but the purely speculative nature of these suggestions can not as yet warrant a longer discussion here.

It should always be borne in mind that the Mendelian analysis is *purely relative.* Baur and Shull and even several others have emphasized this fact when discussing the segregations in their experiments, and Shull has clearly pointed out that it may be quite impossible to indicate whether a particular reaction (character) is due to something positive or to the lack of a factor in the genotypical constitution. All that can as yet be deter-

mined in this regard by Mendelian analysis is the *number of differing points* between the two gametes forming a heterozygote. Such differences may be termed "*geno-differences.*" The well-known facts, that a "character" may be dominant in some hybrids but recessive in others, and that segregation in different cases may be very different, indicate that "characters" are complicated reactions. The famous case of Bateson's fowl-hybrids as to the form of comb may here be quoted as an example: In Walnut comb × Rose comb the latter is recessive, in Single comb × Rose comb it is dominant, and in both cases the segregation gives three dominants: one recessive. Now Bateson has shown that "Walnut" is a compound of Rose- and Pea-comb. Homozygotic Walnut differs from homozygotic Rose only in one point, as does Rose compared with Single. But Walnut-gametes differ from Single-gametes in two points; hence Walnut × Single, with Walnut as dominant, segregates in Walnut, Rose, Pea and Single in the proportions 9:3:3:1. Even with this analysis it is as yet not possible to decide whether Single or Walnut is the form of comb for the realization of which the greater number of *positive* factors are required. Suggesting—what seems to be the most probable assumption—that Walnut is the most geno-complicated case, Single may even be an expression for a multitude of genes in the fowl-constitution. The relativity of the analysis by segregation must in all such cases be remembered, and it is quite erroneous to think that dominance indicates the positivity of the "unit-factor" in question: So "Horns" are in Wood's cases dominant in male sheep but recessive in female sheep. And as to analogs with chemical reactions it must be kept in mind that a characteristic reaction may be the consequence of *lack* of any substance as well as dependent upon the *presence* of any special compound in the solution in question.

The elaborate work of Mendelians of recent years has shown very complicated segregations, and the most specialized segregation is almost the most specialized analy-

sis still known of any "character" in question. The "units" or "unit-factors" stated in Mendelian work are consequently quite provisory, depending essentially upon *the number of genodifferences* in the special crossing. Probably it may be discovered that several such "unit-factors" for one character may also be elements for the realization of quite other characters. If this be the truth, then the present state of Mendelism, characterized by the rapidly augmenting number of new "unit-factors" demonstrated in the organization of different biotypes able to hybridize, may be replaced by a period in which many such unit-factors will be identified. At any rate there is no reason to believe that the further Mendelian analysis will augment the number of genes into absurdity. The enormously increasing possibilities of combinations by augmentation of the number of segregable genes are a source of interest also in this connection.

As to cases of hybridization, in which segregation and combination do not suit the Mendelian "laws," it must at first be stated that some apparent exceptions are probably caused by non-homogeneity of the initial material for experiments. The experiments of Correns, Castle, Miss Saunders, Tschermak and others have shown to excess that phenotypes may seem totally "pure" and nevertheless be heterogeneous (*e. g.*, white flowering stocks or albino mice). Thus constancy as to the phenotype of the progeny is no sure proof for genotypical purity or unity. In discussing alternative inheritance we meet with difficulties of the same nature as in regarding fluctuating variability: the inadequacy of phenotype-description as the starting-point for genetic inquiries.

Secondly, the more or less high vitality of the different combinations of genes in F_2 may perturb the Mendelian results, as Baur has illustrated; in other cases the different degree of facility with which the union of special gametes is realized may influence the relative numbers of representatives in the F_2-generation, as Correns has demonstrated.

Here we can not discuss the difficulties in a complete carrying through of the Mendelian analysis; Bateson's recent book contains a richness of instances concerning this matter. Only one instance of special importance may be mentioned here, viz., the so-called "*blended inheritance*" opposed to Mendelian segregation or "alternative inheritance." In cases of blended inheritance the genes in question might be supposed to "fuse together" by the act of hybridization, or, in accordance with the presence- and absence-view, the gene unilaterally carried to the zygote might here in some manner be "diluted." In this way, which certainly is very badly compatible with the conception of genes as unit-factors, *failing segregation* might be explained.

Cases of failing segregation seemed to be abundant in the beginning of the modern Mendelian era; Mendel himself pointed out some typical cases in the species-hybrids of *Hieracium*. And Correns's indication as to the constant intermediate stature of maize stems seemed to be a crucial case. Now the insight won by breeding experiments as well as by cytological researches concerning the phenomena of *apogamy* has put the question in a new light. The discoveries of Murbeck, Raunkiær, Ostenfeld, Rosenberg and others have led to quite other explanations as to the constancy of several intermediate hybrid forms. In such cases no segregation is realized, because no gametogenesis is going on—and in such cases there is no reason for supposing any "fusing" or "dilution" of genes. And as to Correns's experiments, this careful author has himself withdrawn the suggestion in question.

But still cases of "blending inheritance" remain. Among these Castle's experiences as to the dimensions of rabbits, especially the length of ears, are the most important and most discussed instances. Castle has in a convincing and suggestive manner demonstrated that the complicated color-characters in rabbits agree with the Mendelian laws. Therefore much stress might be laid upon his indication of cases contrary to these laws.

Crossing short-eared and long-eared races, he gained an F_1-generation with almost intermediate ears, and here no segregation was observed in F_2.

But even this case may agree with Mendelian laws. The idea for such interpreting is won—as Lang has clearly pointed out—by means of Nilsson-Ehle's (and East's) experiments, the former concerning the colors of wheat-grains, the latter dealing with the number of "rows" in the ears of maize. Nilsson-Ehle demonstrated that blending of red and white color in wheat is apparently a fiction: The red color is determined by several different genes, acting in the same sense and augmenting the effect of each other. Hence by segregation and new combinations of these approximately equipotent genes a whole series of gradations in red color will be realized. And these gradations must group themselves symmetrically around the phenotype of the F_1 in question. If we have to consider say three genes, A, B and C, we shall for F_1 use the formula AaBbCc, indicating the value 3 which is intermediate between aabbcc as zero and AABBCC as 6. Even in case of no fluctuation such a series must present itself as an almost continuous gradation, and it is not difficult to find out that the progeny of every "class" here will breed true, *i. e.*, the average of the progeny's character will be like the "class" of the parent.

Just so it is in the case of East's experiments with maize, as East himself has clearly illustrated. Thus, well-analyzed instances of heredity in plants, concerning both color-factors and meristic factors may be compared with Castle's case in question. Lang in his interesting criticisms points out that certain irregularities in Castle's F_2-material give strong evidence for the view that we have no blended inheritance but true segregation here as well as in the cases of Nilsson-Ehle (and, as we may add, in the cases of East). Further analysis may then probably demonstrate in a more direct manner the true nature of the apparent blending in Castle's case; as yet we can

only say that this case does not seem incompatible with Mendelian views. It must also be borne in mind that certainly there have been very *many genodifferences* between the differing races intercrossed in Castle's experiments. Hence these experiments are really operating with highly poly-heterozygotic F_1-generations. And how great influence upon dimensions (of ears and other parts of the body) those color-determining genes may have exercised can not be easily determined.

As to beans, it is proved that genes, effective in color-reactions, may also have great influence upon the dimensions and forms. So in my crosses a special factor, which makes yellow color turn into brown and causes violet to be turned into black, has a very marked influence upon the size and form of the beans in question. Here exact data are not necessary; the instance exemplifies the two incident matters of fact, viz., that apparently simple "dimensional" or meristic characters may be determined by *several different genes*, and that one sort of gene may have influence upon *several different reactions*.

Then it seems that Mendelian analysis is proceeding in a very prosperous way; but there may be even very narrow limits for this analysis: the entire organization may never be "segregated" into genes! But still there is much to do in carrying through the genotype-conception as far as possible.

As to cytological researches the genotype-conception is as yet rather indifferent. Certainly the process of segregation must be a *cell-action* intimately connected with division. But all the innumerably detailed results of the refined cytological methods of to-day do not elucidate anything as to segregation. It seems to the unprejudiced observer that the much-discussed cytological phenomena of karyokinesis, synapsis, reduction and so on may be regarded rather as consequences or manifestations of the divisions, repartitions and segregations of genotypical constituents (and all other things in the cell) than as their causes. This view is applicable even in those cases

where sex-determination can be diagnosticated cytologically.

In the discussion as to the existence of true *graft-hybrids* the cytological configurations have of course a high importance as *precisely defined characters* of cells in such cases where the cytological elements of the two species in question are different. And, as it may be well known, cytological evidence is not at all favorable for the idea of graft-hybrids. But the use of cytological configurations for diagnosis is quite different from the idea that special cytological elements might have importance for the phenomena of heredity.

The question of *chromosomes* as the presumed "bearers of hereditary qualities" seems to be an idle one. I am not able to see any reason for localizing "the factors of heredity" (*i. e.*, the genotypical constitution) in the nuclei. The organism is in its totality penetrated and stamped by its genotype-constitution. All living parts of the individual are potentially equivalent as to genotype-constitution. In botany there has been no doubt as to this conception, and as to animals, O. Hertwig has for a long time advocated the same view against the views of Weismann and others, who have suggested that ontogenesis is partly determined or at any rate accompanied by a progressive simplification of the "anlagen" (as we say the "genotype-constitution") in the cells of the growing embryo. The agencies of normally varying ambient conditions and the interactions of specialized parts in the developing individual may exercise their strong influence upon the whole phenotypical state of the resulting particular individual. But these factors will as a rule not change or shift the fundamental genotypical constitution of the biotype in question. Later on we shall touch the problem of such genotypical changes (the mutations) induced by external factors.

Here we have to point out the fact that "living matter"—or, with a more precise definition, those substances or structures the reactions of which we call

"manifestations of life,"—is *inter alia* characterized by the property of *autocatalysis*. The autocatalysis of living beings must embrace the totality of their genotypical constituents. It seems to me that this autocatalysis as well as the *compensative and complemental maintenance of genotypical equilibrium* in the organisms, present some of the greatest enigmas of organic life.

The discussion of cytological problems leads us to the question of *pure or impure segregation*. In the beginning of modern Mendelian researches several instances of presumed impure segregation of genes in gametogenesis were discussed, *e. g.*, as to color factors in animals. But more thorough analytical experiments have in many such cases demonstrated "purity" in the gametes, the characters in question having proved to be more complicated reactions than at first supposed. Recently Morgan has discussed the question in a quite new manner, suggesting —as a working hypothesis—that the segregation might be not of qualitative but of merely quantitative nature. Hence the gametes should as a rule not be pure. Nevertheless, as the author illustrates by means of interesting diagrams, the F_2-generation of a monohybrid with normal dominance might be composed of two classes of individuals sharply defined. And the author suggests that this idea might be able to explain "the graded series of forms so often met with in experience and so often ignored or roughly classified by Mendelian workers."

Here we again touch the question of "blended inheritance." I suppose that the above-mentioned explanations by Lang and East are more consistent with the real nature of the graded series in question. Now the Mendelian work has not only been able to demonstrate that several cases of segregation apparently impure are pure segregations of complicated nature; but even the "spotted conditions" as to color in animals and plants, emphasized by Morgan as a puzzling case, does not seem to present any real difficulty for Mendelian explanation. Certainly such cases as Shull has pointed out, viz., hetero-

zygotic nature being necessary for "mottling" in some special bean-hybrids, may at first glance favor the idea of "spotted conditions" being due to irregular segregation or to different repartition of color-determining factors in the tissues in question. But a closer examination seems to vindicate the real existence of special "spotting factors." The very interesting researches of Lock as to the "Inheritance of certain invisible characters in peas" have clearly pointed out a "spotting" factor or a "pattern"-determiner in peas, independent of any color-manifestation. It must be borne in mind that a multitude of characteristic epidermal "patterns" are found in animals and plants, these patterns concerning all epidermal manifestations and often showing a widely fluctuating variability. As to the realization of all such spots it might be suggested that in neighboring parts of the developing epidermal tissue some little difference of ambient conditions may inhibit or even release reactions, the alternation of which produces the spots.

The whole case seems to be somewhat analogous to the *merely phenotypical phenomena of alternative variability* first pointed out by De Vries, *e. g.*, the alternation of decussated and contorted stems of *Dipsacus*. Here we touch the highly suggestive idea of "*sensible periods*" in ontogenesis or histogenesis emphasized with so good experimental arguments by De Vries. Of course there must be a genotypical fundament for the existence of the alternating character in question, *e. g.*, for the particular nature of the surface of the spots (or for the contortion in Dipsacus, etc.); strains without such genotypical fundament will not be spotted (nor produce contorted individuals at all).—These remarks are made only to point out that Morgan may have exaggerated a little his criticisms as to "spotting factors," but I confess that this question is in need of closer analysis.

Then the problem of pure or impure segregation may still be open; but the tendency in modern genetics goes certainly in the direction of establishing pure segrega-

tion as the normal case. If we accept the suggestion of autocatalysis as an essential factor for the propagation of living matter in general, and hence *eo ipso*, for the growth or multiplication of genotypical constituents, we might in case of impure segregation expect frequently to find "dominants" in the progeny of "recessives"; and the numerical proportions of the dominants and recessives in consecutive generations must be rather irregular. But this is not the case. The recent experiments of Darbishire quoted above demonstrate in a beautiful manner the purity of segregation during subsequent generations in Mendel's classical object, the pea.

Francis Bacon says: "Human understanding easily supposes a greater degree of order and equality in things than it really finds." So we may in modern genetics be aware of the relativity and narrowness of our provisorial explanations, remembering Bacon's warning that "many things in nature may be *sui generis* and irregular!" Among the irregularities in heredity we may reckon the mutations, observed in nature as well as in more precisely defined conditions of artificial experiments. From the famous observations of De Vries and the indications of several earlier authors, to the modern experimental researches of MacDougal, Standfuss, Tower, Blaringhem and others, all evidences as to mutations point out the *discontinuity* of the changes in question. Here we need not enter the question; it is sufficient to state that the essential point is the *alteration, loss or gain of constituents of the genotype*. The splendid experiments of Tower as to *Leptinotarsa* have in the most evident manner shown that the factors which produce the mutations in this case, viz., the temperature and state of moisture, are able to act in a direct manner upon the genotypical constitution of the gametes; and Tower has noted the occurrence of Mendelian segregation in hybridizing his mutants with the original unaltered biotypes. There may in some cases be certain puzzling irregularities to be explained by future researches, but it is evident that in all such muta-

tions, discontinuity is the characteristic feature in the change of type.

As to populations, the biotypes of which may practically exhibit continuous transitions—like the case of my own populations of beans—the idea might be born that biotypes are evolved from each other by extremely small steps in genotypical change. Hence such mutations must be practically identical with "continuous" evolution. But there is no evidence for this view. Certainly in such populations the "static" transitions between the genotypical differences manifesting themselves in several characters may be called continuous—but such a "continuity of museums," as it might be called, is not at all identical with *genetic* continuity. Galton himself has emphasized the capital difference between the notions of continuity in *collections* and continuity in *origin*, and as yet the mutations really observed in nature have all shown themselves as considerable, discontinuous saltations. So in my own still unpublished experiments with pure lines. *Natura facit saltus.* The chemical analog to such mutations may be the formation of homologous alcohols, acids and so on. The greater mutations may be symbolized by more complicated molecular alterations. But such analogs are of very little value for the understanding of genetic evolution.

The genotype-conception supported by the great stock of experiments as to pure line work, Mendelism and mutations does not consider *personal adaptation* as a factor of any genetic importance. Phrases as "characters, won by adaptation and having successively been hereditarily fixed," are without meaning from our point of view. Hence much talk of adaptive characters successively gained seems to us an idle matter. A closer study of desert-organisms and the like may elucidate such things; here the suggestive researches of Lloyd as to stomates in desert plants may be pointed out. And as to the old question of "mimicry," this problem in the famous cases of butterflies has in a most convincing manner been put

into Mendelian terms by the observations and experiments of Punnett, de Meijere and others. This stronghold of the united Lamarckism and selectionism has now been conquered for Mendelism, *i. e.*, for the genotype-conception.

The genotype-conception here advocated does not pretend to give a true or full "explanation" of heredity, but may be regarded only as an implement for further critical research, an implement that in its turn may be proved to be insufficient, unilateral and even erroneous—as all working-hypotheses may some time show themselves to be. But as yet it seems to be the most prosperous leading idea in genetics.

Heredity may then be defined as *the presence of identical genes in ancestors and descendants*, or, as Morgan says in full accordance with this definition: "The word heredity stands for those properties of the germ-cells that find their expression in the developing and developed organism."

And now it is time to end this communication, too long for its real contents, but too short for the importance and diversity of the great problem of heredity.

In concluding this address I must highly emphasize the eminent merits of Hugo de Vries. His famous book "Die Mutationstheorie," rich as well in positive indications as in ingenious views, has been the mediator for the new and the old era in genetics. This monumental work is a landmark in the progress of our science. Like the head of Janus it looks at once forward and backward, trying to reconcile—at least partly—the antagonistic ideas of continuity and discontinuity in evolution and heredity; hence a great deal of the charm of De Vries's work. But just these qualities have made the work of De Vries too eclectic for the stringent analytical tendencies of modern genetics—a tendency which has in recent years found a true home in American science.

THE GENOTYPE HYPOTHESIS AND HYBRIDIZATION[1]

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IT sometimes seems as if the hypercritical attitude had become an obsession among biologists. A proper judicial spirit is of course essential to science, but do not biologists often require a large amount of affirmative data before assenting to a proposition which is in reality a simple corollary of one already accepted?

For example, Darwin emphasized small quantitative variations as the method of evolution, although he recognized the occurrence of larger changes both quantitative and qualitative. De Vries, on the other hand, emphasized large variations—especially qualitative variations—as the real basis of evolution, although he too admitted the existence of lesser changes. He distinctly states that a mutation or new basis for fluctuating variation, may be so small that it is obscured by the fluctuations themselves.

If relative frequency of occurrence is a criterion of the value of variations in organic evolution, which is not necessarily so, Darwin's point of view is probably the nearer correct. If one could find a unit basis for describing variations in terms of the physiological economy of the organism concerned, *i. e.*, if one knew exactly what was a large change and what was a small change, he would probably find that a random sample of inherited variations followed the normal curve of error. By this I

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Contribution from the Laboratory of Genetics, Bussey Institution of Harvard University.

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mean that small variations would center closely around a mode, and large variations would occur with a relative frequency inversely proportional to their size. The point that I wish to emphasize, however, is that neither Darwin nor De Vries recognized the proper distinction between a mutation and a fluctuation. Darwin made no distinction. De Vries, however, considered fluctuations to be linear; that is, to be limited to increase and decrease in characters already present. He thought that selection of such variations brought about changes in the selected population due to the inheritance of the fluctuations, but that the selected populations returned to the mean of the general population after selection ceased. Mutations, on the other hand, were gains or losses of entire characters—qualitative changes—which were transmitted completely, *i. e.*, were constant, from the beginning. De Vries did indeed state that mutations could take place in any direction, which would involve the idea of linear change or quantitative mutations; yet it seems quite evident from his general attitude in "Die Mutationstheorie" that to his mind qualitative and quantitative variations were quite distinct.

Many practical breeders had long known, however, that the selection of linear variations often produced new races which were as constant as any races, provided they were not exposed to crossing with individuals of the general population from which the selected race had come. Why this was true was unknown. It was felt that there was a real distinction between certain variations, to which Darwin had not called attention; yet it was felt that the De Vriesian idea was not wholly correct. It has been in making this distinction clear-cut and definite that Johannsen has rendered his great service. His elaborate extensions of the genotype conception of heredity have cleared up many debated points, and corroborative evidence has been received from so many lines that it can hardly be doubted that the main points of the hypothesis are correct. It may seem, therefore,

as if the superstructure of this conception were too elaborate to rest upon a simple foundation; yet I can not see but that the basis of the entire hypothesis is the fact that a fluctuation is a non-inherited variation produced upon the soma by environmental conditions, while the inherited variation, the mutation if you will, is any variation qualitative or quantitative, that is germinal in character. This being so, it seems scarcely necessary for an elaborate proof of the proposition, for it is nothing but a corollary to that part of Weismannism which was already generally accepted.

Of course it is recognized that pure Lamarckism still has followers to whom neither Weismannism in any form nor the genotype conception of heredity could appeal. But to thorough Weismannians and to those who believe in occasional germinal response to environmental conditions, it seems as if both propositions must be acceptable and their interdependence apparent.

Let us follow this line of reasoning to its logical conclusion in regard to the physiology of heredity. The Mendelian notation has been generally accepted as a convenient way of accounting for the facts of heredity in certain markedly discontinuous characters. It has been questioned by many, however, whether the Mendelian conception is not rather an apparent interpretation of a relatively small number of facts than a general law. De Vries has even suggested that there are definite physiological reasons why certain characters should Mendelize and others should not. His idea is that Mendelian segregation occurs when a germinal determinant for a character (*Anlage*) meets an opposing determinant, and when no such opposition exists the character in the cross-bred organism breeds true. Now the universal tendency of the facts of breeding is towards an interpretation the opposite of this. When a determinant from one parent meets with no such determinant from the other parent (presence and absence hypothesis), Mendelian segregation appears. When the same determinant is received from

both parents, segregation can not be proved, for the character breeds true.

In fact the many results of experimental breeding during the past few years have convinced me that De Vries's general conception of this matter is incorrect. There may be finally a considerable modification of our ideas regarding the ultimate nature of Mendelian unit characters and the exact meaning of segregation, yet the universal applicability of a strict Mendelian system to interpret the facts of heredity becomes more and more apparent every day. And the point that I wish to emphasize is that Mendelian inheritance is a genuine corollary of the genotype hypothesis if the latter is applicable to a population in a state of natural hybridity. In my work with maize where free intercrossing does occur I am convinced of the existence of genotypes in a state of natural hybridization. Furthermore, these genotypes can be isolated by inbreeding. If it were true, then, that only certain markedly discontinuous characters such as color Mendelize, how could genotypes which differ from each other in size characters be isolated? It is not expected, however, that the statement that Mendelian inheritance and the genotype hypothesis are interdependent will be received without proof. Data that are believed to furnish such proof are submitted here.

When Mendelism was a new idea it was natural that the behavior of many hybrids should be regarded as irreconcilable to such a system of interpretation. The earlier criticisms arose largely through the misconception that dominance instead of segregation was its essential feature. Later, when so many complex results from pedigree cultures were fitted into a strict and simple Mendelian notation, it was objected that the investigators could by expert juggling of a sufficient number of factors interpret according to their system any experimental results they might obtain. Perhaps a few biologists regarded as a personal affront the gradual growth of the idea that the facts of heredity were complex, but it is

hardly likely that many could regard this complexity as an invention of Mendelians. The latter would only too gladly have the facts as simple as possible.

There have remained, however, several instances in which hybrids apparently did not segregate in the F_2 generation. Mendel himself investigated one such case, the genus *Hieracium*. The investigation of Ostenfeld[2] made this case perfectly clear by showing that the hybrids reproduced apogamously. Such asexual reproduction may also explain the behavior of hybrids between species of brambles which are also said to breed true in all their characters. These cases, however, and others among animals of which human skin color is the example *par excellence*, may be left out of consideration because no exact data concerning them have been forthcoming. There remain the experiments of two careful investigators who observed no segregation in the F_2 generations of their hybrids, those of Lock[3] upon heights of maize plants and those of Castle[4] upon weights and ear lengths of rabbits. Lock expected that if segregation occurred it would be into two classes, *i. e.*, simple mono-hybridism. For this reason he made no measurements which would show whether he obtained the kind of segregation which as is shown later in this paper, does occur in maize hybrids. Castle[5] has recently admitted the possibility that his numbers were not large enough to prove definitely that segregation involving several small unit characters does not occur in the ear length of rabbits.

The difficulty attending this earlier work was that there was no way of explaining different manifestations of the same character. Segregating characters could always be interpreted either as the presence and absence of a unit

[2] Ostenfeld, C. H., 1904, "Zur Kenntnis der Apogamie in der Gattung *Hieracium*," *Ber. Deutsch. Bot. Ges.*, 22: 7.

[3] Lock, R. H., 1906, "Studies in Plant Breeding in the Tropics," III, Experiments with Maize, *Ann. Roy. Bot. Gard. Peradeniya*, 2: 95–184.

[4] Castle, W. E., *et al.*, 1909, "Studies of Inheritance in Rabbits," Carnegie Inst. Wash. Pub., 114: 5–70.

[5] In lectures at the Lowell Institute, Boston, Mass., 1910.

giving a 3:1 ratio, or as the complemental action of two different units each allelomorphic to its absence, giving 9:3:3:1 ratios or modifications of them. Nillson-Ehle[6] and the writer,[7] however, have shown that several units each allelomorphic to its own absence may be the determinants of what appears to the eye as a single character. In the above paper the writer suggested that if such ratios as 15:1 and 63:1—di-hybrid and tri-hybrid ratios, respectively—were found in considerable numbers, then higher ratios of this kind might account for the apparent constancy of hybrids in characters that seemed to be continuous. For, if—as is quite probable—the additional units increase the activity of the character in question, and if there is no dominance,[8] it is quite evident that hybrids may be intermediate between the two parents. All the pure classes in a complex character of this kind would indeed be difficult to isolate, but segregation could be absolutely proved by a comparison of the variability of the F_1 and F_2 generations.

Since writing the above paper I have obtained clear evidence of 15:1 ratios in two other cases. The first is a red pericarp color, the second is the condition of endosperm in maize which gives dented seeds as distinct from that which gives flinty seeds. There is even considerable probability that higher ratios occur which affect the latter character. In another paper[9] I have shown photographic evidence of size segregation in varieties of *Nicotiana rustica* and stated that similar evidence of segregation of size character in maize had been obtained. The following figures and tables show sufficient of the evidence from the maize crosses to demonstrate conclusively

[6] Nillson-Ehle, H., 1909, "Kreuzungsuntersuchungen an Hafer und Weizen," *Lunds Universitets Årsskrift*, N. F., Afd. 2., Bd. 5, Nr. 2. 1–122.

[7] East, E. M., 1910, "A Mendelian Interpretation of Variation that is Apparently Continuous," AMER. NAT., 44: 65–82.

[8] One dose, *i. e.*, receiving the same gene from a single parent, would on the average increase the manifestation of the character half as much as two doses.

[9] East, E. M., 1910, "The Rôle of Hybridization in Plant Breeding," *Pop. Sci. Mon.*, Oct., 1910, pp. 342–354.

that size characters segregate. It is hoped that this evidence will make us more cautious about accepting uncorroborated statements about characters which are definite exceptions to the Law of Mendel. It is by no means certain that no such exist, but no experimental proof of hybrids non-Mendelian in character has been made.

A further proof of segregation of size characters has recently been made in a preliminary note by Emerson.[10] He states that definite segregation occurs in beans, gourds, squashes and maize. His full data are therefore awaited with great interest.

Table I shows the frequency distribution of the heights of plants in a cross between no. 5 a medium-sized flint maize and no. 6 a tall dent maize. Sufficient seed was obtained in a previous season so that the entire series could be grown in rows side by side during one summer. This procedure eliminates any possibility that the variability of the F_2 generation might have come from varying conditions of soil fertility.

It will be noticed that the F_1 generation is nearly as tall as the taller parent. This increase in size is not due to dominance. It is the increased vigor that comes from crossing in maize, and while it obscures the hereditary differences in size, it is really a problem of development and not of heredity as was shown in a previous paper.[11]

The distribution of heights in the F_2 generation is seen by simple inspection of the table to be more variable than the F_1 generation in the case of each ear planted. Reduced to simple terms by the calculation of the coefficient of variation in each case, however, the two generations can be compared more accurately. In the F_1 generation the $C.V. = 8.68 \pm .553$ while in the various F_2 generations from different ears the coefficients of variation run from $12.02 \pm .559$ to $15.75 \pm .684$.

[10] Emerson, R. A., 1910, "Inheritance of Sizes and Shapes in Plants," AMER. NAT., 44: 739–746.

[11] East, E. M., 1909, "The Distinction between Development and Heredity in Inbreeding," AMER. NAT., 43: 173–181.

TABLE I [12]

FREQUENCY DISTRIBUTION OF HEIGHTS OF MAIZE PLANTS IN CROSS (5 × 6)

No.	Class Centers in Inches for Heights of Plants																					A.	S.D.	C.V.
	51	54	57	60	63	66	69	72	75	78	81	84	87	90	93	96	99	102	105	108	111			
5	3	2	4	5	11	17	17	18	10	6	4											68.22 ± .406	6.49 ± .324	9.51 ± .421
6													1	2	2	13	14	16	14	8	3	101.18 ± .400	5.07 ± .283	5.01 ± .279
(5 x 6)- F_1											5	4	3	9	9	6	5	4	4	7		94.53 ± .740	8.21 ± .519	8.68 ± .553
(5 x 6)- 1 F_2	2	1	3	6	3	5	10	10	22	16	10	7	11	13	6	10	8	4	4	2		81.00 ± .685	12.76 ± .486	15.75 ± .684
(5 x 6)- 2 F_2				2		2	4	2	6	5	12	8	12	6	5	8	3	10	8	2	2	88.33 ± .802	11.78 ± .567	13.34 ± .675
(5 x 6)- 8 F_2	2				4	4	12	7	9	13	12	15	10	8	8	1	1	1				79.46 ± .621	9.55 ± .438	12.02 ± .559
(5 x 6)-14 F_2		1	2	4	2	7	8	17	21	11	27	24	16	9	11	10	5	4	2			81.24 ± .513	10.28 ± .364	12.65 ± .450

TABLE II [13]

FREQUENCY DISTRIBUTION OF HEIGHTS OF PLANTS IN CROSS (54 × 60)

No.	Class Centers in Inches for Heights of Plants																							Total
	22	25	28	31	34	37	40	43	46	49	52	55	58	61	64	67	70	73	76	79	82	85	88	91	
No. 54													2	6	10	17	24	26	21	14	14	7	3	1	145
No. 60	←———	———	———	———	———	———	——→ [14]																		100
(60-5 x 54) F_1														←———	———	———	———	———	———	———	——→ [14]				55
(60-8 x 54) F_1											←———	———	———	———	———	———	———	———	———	———	———	——→ [14]			26
(60-3 x 54) F_1												←———	———	———	———	———	———	———	———	———	———	——→ [14]			30
(60-5 x 54) F_2 [15]						2	2	1	8	18	26	44	95	117	126	92	59	31	22	3	3				649
(60-8 x 54) F_2 [16]						1		1	5	6	13	13	35	29	36	27	21	20	9	6	4	1	1		228
(60-3 x 54) F_2 [17]						5	15	13	32	31	68	60	72	34	47	14	13	5							409

[12] Grown side by side in same season.

[13] Distributions giving figures grown side by side in same season.

[14] Extremes were measured and number of plants counted. All were strongly convergent around the central classes.

[15] Grown from five different ears.

[16] Grown from two different ears.

[17] Grown from three different ears.

Table II shows a similar distribution of heights in cross between no. 60, a dwarf pop maize commonly known as Tom Thumb, and no. 54, a sugar corn known as Black Mexican. The distribution of heights of no. 54 was obtained in the same season as the F_2 generation. They were both grown upon the same plot of ground in which the soil appeared to be quite uniform. Unfortunately, the exact distribution of the heights of no. 60 and of the F_1 plants which were grown in previous seasons, is unknown. The range of the variates shown by the black lines, however, is correct. Furthermore, from notes recorded at the time we know that the F_1 generation was comparatively uniform, the greater number of variates being distributed around classes 67, 70 and 73 inches. In this case, also, the effect of crossing is shown by the relatively high plants of this generation. The plants of the F_2 generation show a wide range of variation. The highest individuals are practically the height of the highest individuals of the taller parent, no. 54. The lowest plants of F_2 do not reach the lower range of no. 60. I interpret this as due to continued heterozygosis in other characters and to physiological correlation. By the latter term I mean that since the plants of no. 60 are very small, F_2 segregates of the same size could only be expected where the ears and seeds also are very small. But since the ears and seeds of these plants also show segregation in new combinations, normal growth correlation probably resulted in a somewhat larger average size. For example, little 40-inch plants were found with ears three times the length of normal ears of no. 60. It is likely that such plants might have been smaller if they had been recombined with the characters necessary for the production of smaller ears.

Table III and Figs. 1–4, show the lengths of ears in the cross just described. In making this table the best ear from each plant that bore a well-filled ear was taken. The small ears, therefore, do not represent poor, unfilled or supernumerary ears. The coefficients of variability

TABLE III[18]

FREQUENCY DISTRIBUTION OF LENGTHS OF EARS IN CROSS (60 × 54)

No.	Class Centers in Cm. for Lengths of Ears																	A.	S.D.	C.V.
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21			
No. 60	4	21	24	8														6.6±.073	.81±.051	12.27±.783
No. 54									3	11	12	15	26	15	10	7	2	16.8±.121	1.87±.088	11.13±.531
(60–5 x 54) F_1					1	12	12	14	17	9	4							12.1±.121	1.51±.088	12.48±.722
(60–5 x 54) F_2 [19]			4	5	22	56	80	145	129	91	63	27	17	6	1			12.7±.058	1.99±.037	15.67±.296
(60–8 x 54) F_2 [20]			1	10	19	26	47	73	68	68	39	25	15	9	1			12.9±.076	2.25±.053	17.44±.413
(60–3 x 54) F_2 [21]			2	5	17	33	33	33	27	21	13	10	11	12	1	2	1	12.6±.128	2.81±.087	22.30±.744

TABLE IV

FREQUENCY DISTRIBUTION OF WEIGHTS OF SEEDS OF CROSS (60 × 54)

No.	Class Centers in Grams for Weights of 25 Seeds																				A.	S.D.	C.V.
	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5			
60	7	22	28	4																	2.7 ± .034	.31 ± .024	14.44 ± .899
54									2	2	5	7	14	10	5	4	1	2	1	2	8.3 ± .107	1.21 ± .074	14.54 ± .963
(60–5 x 54) F_1				5	12	13	17	4	3												4.6 ± .059	.64 ± .041	13.91 ± .912
(60–5 x 54) F_2 [22]		1	7	17	49	98	113	83	69	43	27	13	8	1		1					5.3 ± .032	1.09 ± .022	20.56 ± .442
(60–8 x 54) F_2 [23]				1	3	15	16	17	23	23	18	12	8	9	1	1					6.2 ± .067	1.23 ± .047	19.84 ± .799
(60–3 x 54) F_2 [24]				4	10	24	41	53	40	52	21	19	9	8	2	3					6.0 ± .047	1.17 ± .033	19.50 ± .563

[18] No. 60 and F_1 gen. grown in 1909, No. 54 and F_2 gen. in 1910.

[19] Grown from five ears.

[20] Grown from two ears.

[21] Grown from three ears.

[22] Grown from five ears.

[23] Grown from two ears.

[24] Grown from three ears.

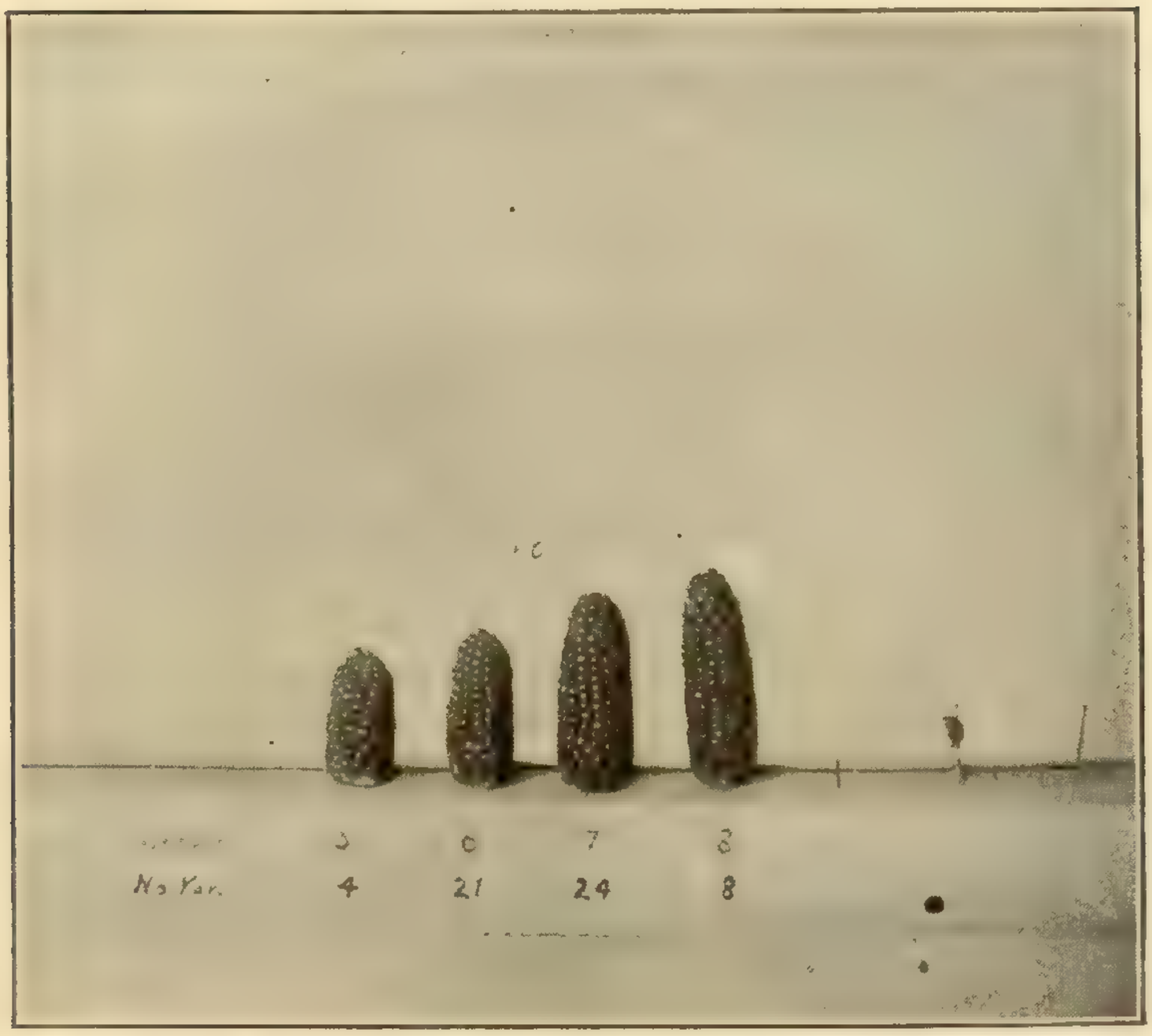

FIG. 1. No. 60, female parent, illustrating variation in length of ear ($\frac{1}{8}$).

have again been calculated, but they hardly emphasize the real segregation as well as do the photographs which were made from representative ears of the different classes found in the actual crop.

Table IV shows the segregation of weights of seeds in F_2 in this same cross. Fig. 5 shows the average size of

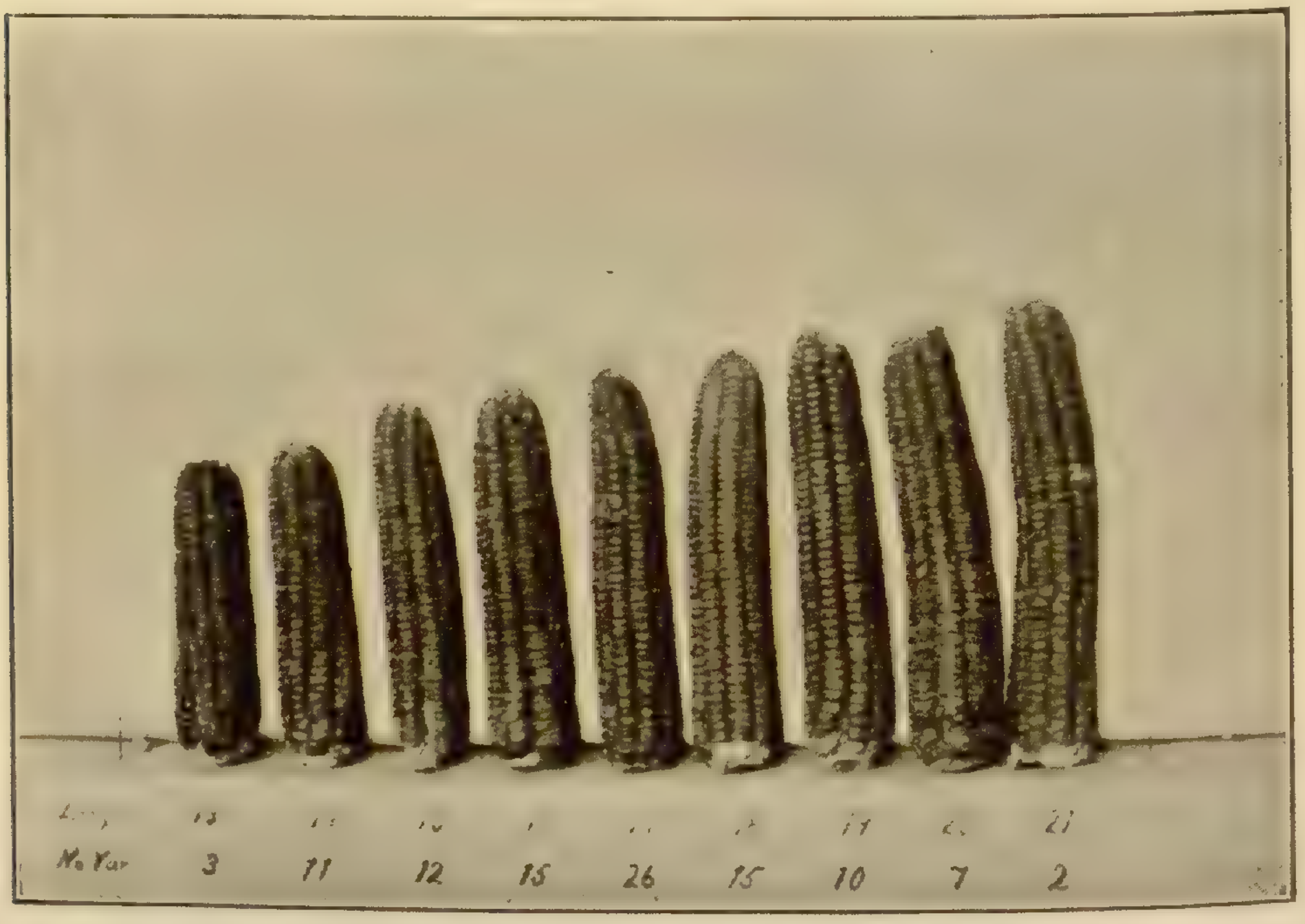

FIG. 2. No. 54, male parent, illustrating variation in length of ear ($\frac{1}{6}$).

FIG. 3. Variation in length of ear of F_1 generation of cross between No. 60 and No. 54 ($\frac{1}{8}$).

the seeds of the two parents and the F_1 generation and the extremes of the F_2 generation. In making the weights for this table, it was necessary to use a scheme by which the sugary wrinkled seeds of the Black Mexican parent, no. 54 could be weighed as starchy seeds. This

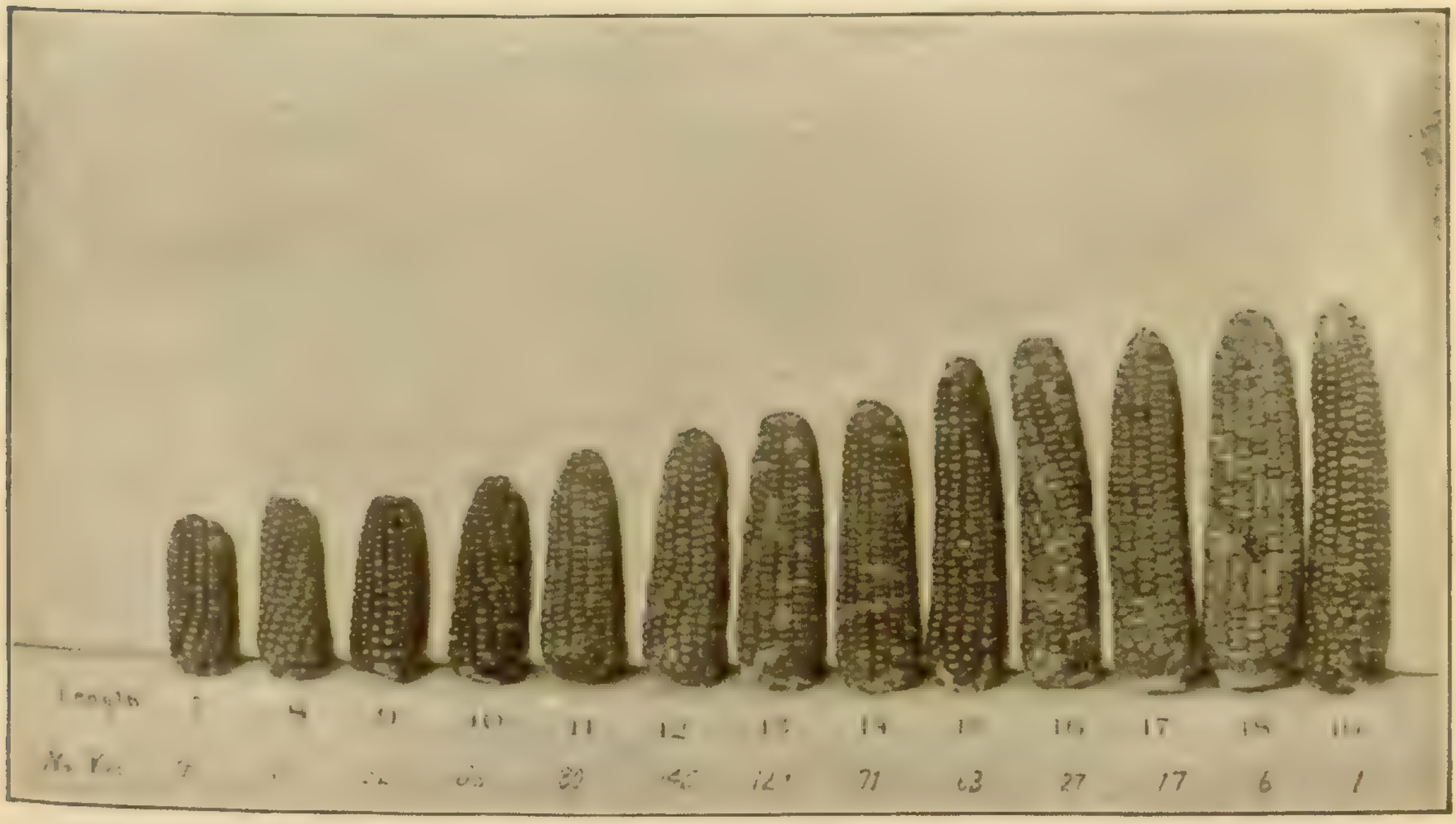

FIG. 4. Variation in length of ear of F_2 generation of cross between No. 60 and No. 54 ($\frac{1}{8}$).

was done by planting the no. 54 between rows of the hybrid. Sufficient crossed seeds which had become starchy through *Xenia* were obtained to make the weights given. Not all of the ears, however, had 25 starchy seeds, which accounts for the small number of plants measured. Furthermore, the seeds of no. 54 were a rather mixed lot, which of course resulted in a higher variability than would probably have been found if only seeds

FIG. 5. Average size of seeds of No. 60 and No. 54 and the F_1 generation of the cross between them. Extremes of the F_2 generation.

of the individual plant of no. 54 which was used as the male parent of the cross, could have been planted. Perhaps it should be noted here since the question might arise, that since the size of the seeds on an ear is governed by the development of the pericarp, the sugar corn, no. 54, was unaffected in other ways than by having the pericarp filled out with starch by the hybridization which occurred attended by the resultant *Xenia*.

In Tables III and IV the measurements and weights of the F_1 generation were recorded from only one cross, although three crosses between the two varieties were made. It might be said that one has the right to com-

pare only the F_2 generation of cross of which the F_1 generation is given. If this were granted our conclusions in regard to segregation would be the same. It might be said, however, that sufficient records were made of the F_1 generations of the other crosses to know that they differed but little from the family of which the data were recorded. In addition, it is a fact that general

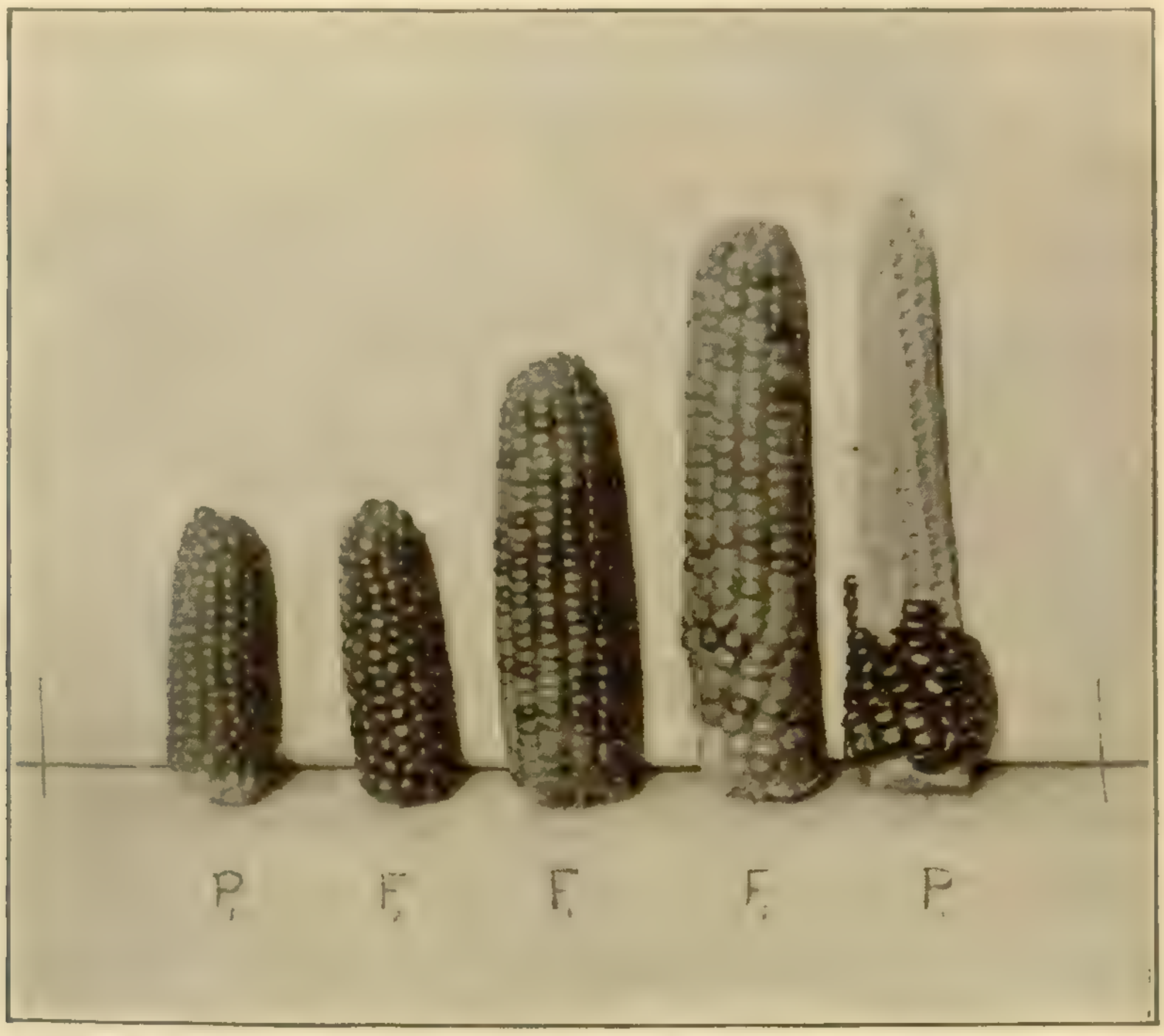

FIG. 6. Average ears of No. 60 and No. 38 and the F_1 generation of the cross between them. Extremes of the F_2 generation.

populations of the two parents were studied, and their variation was undoubtedly greater than would have been that of the inbred progeny of the three parent plants of either variety.

An additional cross between Tom Thumb pop maize and a small purple flint is illustrated in Fig. 6. The ears pictures show the average size of the two parents and the F_1 generation, and extremes of the F_2 generation.

In conclusion there are two points I wish to notice. Unquestionable segregation in size characters has been shown by comparison of the F_1 and F_2 generations. It can scarcely be doubted that some of these segregates will breed as true as the parent forms, yet one can

scarcely do more than speculate in regard to the specific characters that are concerned in developing either organs or individuals of certain sizes. There are probably many characters that interact together in developing certain characters, although the actual determinants in the germ cells may be transmitted independently. These interdependent reactions during development obscure to us the real causes and what we regard as independent characters may be but indirect results of unknown causes. For example, the ability to evert their starch when heated has been the distinguishing character of the subspecies called *Zea mays everta,* the pop maizes. This character so called, however, is the resulting physical condition of the starch caused at least partially by the small size, the thickness and the toughness of the enveloping pericarp.

For these reasons it may not be possible—at least very soon—to point out even the number of characters concerned in size developments. From the number of extreme segregates obtained in each case I might venture to state that the size of ear in the cross shown in Fig. 5 is apparently due to not less than three characters, while the size of ear in the other cross pictured seems to be due to not less than four characters.

NOTES ON GUNDLACHIA AND ANCYLUS

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About seven years ago,[1] in the *Nautilus* I called attention to certain problems connected with the genera mentioned in the title of this paper, and urged investigation of the subject from the hypothetical view of the two following propositions:

1. That *Gundlachia* is merely an *Ancylus* which under favorable circumstances has been able to form a calcareous epiphragm and survive the winter, which ordinarily kills the great mass of individuals, and, while retaining the shell of the first season, to secrete an enlarged and somewhat discrepant continuation of it during the second summer.

2. That not all Ancyli necessarily have the ability to do this, but the practise may have developed in certain small species; and in tropical regions where the dry season takes the place of winter it is possible that survival may become more or less habitual with some of these species.

In this connection attention may be recalled to the æstivation in dry mud behind a double epiphragm, in the Bahamas, of *Segmentina dentata* Gould,[2] and to the observations of Erland Nordenskjold[3] on *Ancylus moricandi* Orbigny, in Brazil.

During the past four years I have received an interesting series of notes by Mr. John A. Allen, of Cleveland, Ohio, connected with the Nungesser Electric Works of that city, who has for some time been domesticating in small aquaria species of fresh-water shells, including

[1] *Nautilus*, XVII, No. 9, pp. 97–98, January, 1904.

[2] Smithsonian Miscell. Coll., Vol. 47, Pt. 4, No. 1566, pp. 446–448, April, 1905.

[3] *Zool. Anzeiger*, XXVI, pp. 590–593, July, 1903.

Ancylus and *Gundlachia*. His observations extend over some six years and his notes contain so much of interest that it has seemed desirable to summarize and publish his data, thus placing on record facts which may stimulate others to follow his example.

Mr. Allen was kind enough to send to the museum a lot of *Anacharis* supposed to contain both *Ancylus* and *Gundlachia* in the living state, and numerous specimens of the former were observed in a jar to which the vegetation was consigned, immediately after it was filled with water. We were not able to distinguish with certainty any *Gundlachia*, though some may have been present, and the small aquarium was kept in good condition to await developments. This was in December, 1907. The Ancyli continued to exist in apparent health during the winter. In May, 1908, they seemed to go into hiding, but during the summer reappeared again in rather diminished numbers, while a few young ones were observed. No particular change was noticed during the following winter and spring. While absent during the summer of 1909, it became necessary to transfer the collections to the new building of the National Museum and the aquaria were set aside. After the confusion of the transfer was measurably over, I examined the aquaria and, finding nothing visible, had the contents of the smaller one (about $8 \times 4 \times 10$ inches in size) removed and submitted to the most careful scrutiny, the sand at the bottom being placed in a fine sieve for examination, but not a trace of *Ancylus* remained. I concluded that there had been sufficient carbonic acid in the water to completely dissolve these fragile shells after death, and that some unfavorable condition had exterminated the colony. In the other aquarium, which was about eight times the capacity of the smaller one, the water had evaporated to about half its normal quantity and no mollusks except a few small Lymnæas were visible, while the *Anacharis* had suffered considerably by the adverse conditions. This was towards the end of November, when it was

difficult to get any fresh weed except by purchase. Being much occupied, I contented myself with having the aquarium filled with Potomac water from the tap. A short time afterward I was surprised to note a large number of young *Ancylus* with clean translucent shells, on the side of the tank. There had never been any *Ancylus* in the aquarium except such as might have been put in with Mr. Allen's *Anacharis*. These had up to February 22, 1910, grown rapidly and continued to flourish, though the number then visible was only about half that which was noticed in November. In April the *Ancylus* completely disappeared again. I have not been able to discover where they went to, as the most careful scrutiny of the sparse amount of *Anacharis* remaining has not revealed any on the stems or leaflets. None of the specimens seemed to have formed any septum and nearly all of them were carrying a small colony of five or six minute hydroids on the posterior upper surface of the shell. The shells in February were still too fragile to admit of removal from the glass without crushing, and most of them kept on the side away from the window, on the sill of which the tank stood. They were about 3.0 mm. in length, and remarkably active, moving about on the glass with surprising speed.

Subsequently Mr. Allen kindly furnished me specimens of all these stages in alcohol; and I also had the opportunity of seeing some specimens in alcohol which had been sent to Mr. Bryant Walker and Dr. H. A. Pilsbry in 1908, and which were obviously identical with those sent as examples by Mr. Allen to me over a year later, and Dr. Pilsbry thought also with specimens collected at Rockford, Illinois, in the ancyloid stage. On account of its relations to the *Gundlachia* it will be referred to here as *Ancylus meekiana*, since, unless in the *Gundlachia* stage, it seems not to have been described.

Mr. Allen also sent a lot of the wild *Ancylus* collected in the Thornburg lagoon and which he was disposed to regard as something distinct from his aquarium ancy-

loids. After a careful examination under the microscope I have been unable to find any constant differences between shells of the same age, except that the larger specimens of *Ancylus* seem to have grown continuously and evenly, while those ancyloids which attained a *Gundlachia* stage show the sharp contrast between the separate stage and that with the expanded third stage of the shell. As this is only what one might expect if the *Ancylus* attained its full growth without interruption, while the ancyloid becoming septate passed through a resting stage and then began to grow again, I consider this difference of no moment systematically. The young *Ancylus* and the ancyloid of the same length appeared generally quite identical, though I noticed that in both the obliquity of the apex varied to some extent, being more emphatically bent toward the posterior right side in some individuals than in others.

Ancylus meekiana is, when young, for a time nearly parallel-sided, the growth toward maturity being more expanded than at first. The apex is behind the middle of the shell and slightly inclined toward the posterior right-hand side at maturity. The microscope reveals some very feeble radial striæ from the apex, mostly vanishing before they reach the base. The incremental lines are not strongly marked and the shell when clean is of a pale translucent yellowish color. At or near maturity the shell assumes a more oval form slightly more expanded in front than behind. The animal has short pointed tentacles, well-marked black eyespots, and a bluish-white color, except about the mouth, where the yellow-brown jaws are laterally set and the buccal mass has a pinkish color. The shell is about 3.6 mm. long, 2.3 wide, and 1.0 high. In the dark-colored specimens of the wild *Ancylus*, on the inside, may often be seen a dark-brown line corresponding to the margin of the young *Ancylus* and showing the more parallel-sided early outline.

Miss Mary Breen, who has been studying the anatomy of the fresh-water gastropods of the District of Co-

lumbia, was kind enough to undertake the removal and mounting of radulæ taken from specimens of the different stages, as well as from the wild *Ancylus*. This was a task of no little difficulty on account of the extremely minute size of the organ. The radulæ of ancyloids, septates and *Gundlachia* were absolutely identical in appearance and in number of teeth, the formula 5·10·1·10·5, holding good for all. The uncinal teeth are not gradually modified from the laterals, but change abruptly and form a distinct band on each side of the radula. The lateral part of Stimpson's figure of the dentition of his *Gundlachia meekiana* is imperfectly made out, and obviously inaccurate; due doubtless to the fact that he had only a few specimens and a not very powerful microscope. Unfortunately his original material was destroyed in the great fire at Chicago of 1871.

An examination of the radula of a septate form, collected in Nicaragua by Professor B. Shimek, showed a similar radula but with one more uncinal tooth on each side. In this case, unfortunately, while endeavoring to transfer the minute object to a slide for permanent preservation, it mysteriously disappeared, and a trial with a second specimen was no more successful.

The form of the laterals is fairly well given by Dr. Stimpson, and the rhachidian tooth is correct in his figure; but the gradual modification and uncertain number of the outer teeth of the radula do not agree with our observations on the specimens from Ohio. Renewed correspondence with Mr. Allen led to the preparation of this paper, pending the continuation of his observations.

Since the different stages of *Gundlachia* need to be carefully discriminated, I have adopted the following nomenclature for them.

In the first stage, when the young shell has a laterally compressed subconical shape without any trace of septum, and is to all intents and purposes, concholog-

ically and anatomically, an *Ancylus*, I call the individuals "ancyloids."

In the second stage when the base of the conical shell is more or less closed by a flat horizontal septum continuous with the margin around it, I call the individuals "septates."

Lastly, when the animal in its second season begins to form a marginal expansion external to the septum, and with its longitudinal axis sometimes at a considerable angle with the axis of the ancyloid shell, I reserve for this stage, up to and including maturity, the term "*Gundlachia*."

Mr. Allen kindly sent alcoholic specimens of ancyloids, septates and *Gundlachias* from his aquarium for anatomical examination. The posterior part of the foot entirely hides the septum when the living animal on the walls of the aquarium is examined through the glass. Nothing to distinguish it from ordinary *Ancylus* is visible in the soft parts. The creatures feed on the microscopic algæ, etc., which grow on the walls of their domicile and when feeding the movement of the jaws and radula can be seen with ease by means of a magnifier. On the alcoholic specimens, on the exterior of the shell, were many minute lenticular capsules which, from analogy with *Neritina*, *Pompholyx*, etc., were supposed to be the ovicapsules. The very young shells are very transparent and fragile. It is difficult to find them until they have reached a length of over a millimeter, and so far it has proved impracticable to detach them from their roost without crushing them, they are so extremely fragile. The smallest septate seen was slightly less than two millimeters in length and the animal had entirely withdrawn behind the septum, which covers more than two thirds of the aperture.

The species in the *Gundlachia* stage agrees substantially with the form described from the District of Columbia by Stimpson, under the name of *Gundlachia meekiana*. As in many other fresh-water shells the newly

formed shell is yellowish translucent, while the older part, especially when the pond or aquarium has a muddy bottom, often becomes darkened or even blackish, and more or less covered by a growth of conferva. Mr. Allen calls attention to the fact that the sharp line of demarkation which separates the dark encrusted shell of the septate from its translucent *Gundlachia* extension in the final stage, is evidence that the growth is not continuous, but that a resting period of some duration separates the two stages.

I have preferred for the most part to refrain from theorizing on the inferences to be drawn from the data, letting them speak for themselves. To me, however, the facts tend strongly to confirm the hypothesis suggested in the opening paragraphs of this paper.

General Notes

The following notes are partly summarized from a rather voluminous correspondence with Mr. Allen, extending over more than four years.

The Thornburg lagoon is an abandoned channel of the Cuyahoga River. In 1903 the river was fairly well stocked with Unionidæ, but soon after that date the contamination of the river by drainage and sewage killed off the naiad population. This contamination is not believed by Mr. Allen to have seriously affected the water of the lagoon, though for some reason it does not seem to be a place favorable to vigorous growth of mollusks. It produces a dwarf *Planorbis parvus*, a poorly developed *Physa*, a small form of *Lymnæa humilis modicella* and a scanty supply of *Amnicola*. It is nearly filled with *Nuphar* on the leaves of which *Ancylus* is found; also *Ceratophyllum*, *Potamogeton*, etc., occur, especially where the water is shallow.

At one place the bank bordering on the lagoon is steep and the water near it deep, so here even at low water mollusks would never be left dry. There is another portion of the lagoon where a wide zone, producing vegeta-

tion on which *Ancylus* occurs, is sometimes left uncovered when by dry weather the water becomes low. In this part of the lagoon three *Gundlachia* were found. In general the water of the lagoon is deep and constant, but owing to the presence of these shallows the hypothesis that the formation of a septum in *Gundlachia* may be due to alternation of wet and dry periods can not be wholly excluded.

Ancylus occurs in one to three feet of water where *Ceratophyllum* is abundant. In the deeper water shore there is more *Nuphar* and less fine vegetation the *Ancylus* seems to be absent or rare.

Mr. Allen attempted to domesticate the Thornburg *Ancylus*, placing many young ones in a 15 × 9-inch jar stocked with *Anacharis* from the lagoon. Apparently, all soon disappeared, although *Lymnæa* and *Amnicola*, coincidentally transferred, lived a long time.

NOTES ON THE SEVERAL JARS USED AS AQUARIA

The 15 × 9-inch Jar.—This originally contained a dwarf *Nymphæa* which died. There was a mixture of peaty and ordinary soil about three inches deep in the bottom of the jar. This was stocked in 1906 with *Anacharis* and some specimens of *Vivipara*. The date of the first appearance in it of the ancyloid stage of *Gundlachia* was not determined. February, 1907, individuals were very numerous and, some being taken out to save in the dry state, the septate form was discovered. Mr. Allen had noticed the presence of the ancyloid form some time before. The first date at which *Gundlachia* had been obtained from the Thornburg lagoon was July 15, 1906, but Mr. Allen doubts if the copious swarm of ancyloid individuals of *Gundlachia* could have originated in the jar so quickly from individuals accidentally put in at that time. Some of the vegetation in the jar had been received from elsewhere in Ohio, and some from another state. The ancyloid stage of the *Gundlachia* can not be distinguished from the associated *Ancylus* by

the external features as seen in the aquarium. In February, 1907, probably hundreds of the unseptate ancyloid form were present. There were several *Vivipara* in the jar that winter. Subsequently they were removed, Mr. Allen thinking that they might consume the food supply needed by the ancyloids. Having heard that the stunted growth of aquarium mollusks might be due to the presence of their soluble excreta in the water, he thought the removal of the *Vivipara* might have had some influence in this way. However, the removal of the large snails did not stop septation.

In the winter of 1906–07 the specimens of *Planorbis parvus* in the jar were large and healthy. In the winter of 1907–08 the individuals of this species appeared dwarfed. The water in the jar was then removed and replaced by distilled water. After that the *Planorbis* (and Mr. Allen thought also the *Anacharis*) took on a more healthy appearance. He thought that the concentration of saline matter due to refilling loss from evaporation with ordinary lake water might have been influential injuriously, and the transfer to distilled water have lessened the tendency to septation.

In the winter of 1907–08 septate individuals of which the exact number were not recorded were again found in the jar. In January and February, 1908, the ancyloid form was fairly plenty, though not so numerous as in the previous year. In spring they became fewer and in May, 1908, there were none visible (although in a smaller jar there were some). They reappeared in the first half of June, 1908. July 3, 1908, an immature septate individual was taken, and another on July 20. On the theory that the septum is formed during a resting stage, these may have been forming during May, when nothing was in sight. August 3, 1906, another specimen was taken. January 11, 1909, a specimen was found which had begun to add the third or expanding stage of the shell external to the septum. No mature *Gundlachia* were taken from this jar during the winter of 1908–09.

August 19, 1909, a minute ancyloid specimen was taken, and another August 24. September 26 six ancyloids were visible at one time, but were not disturbed. It was noticed that the ancyloids came out in sight on the walls of the jar more freely on cloudy than sunny days.

This jar, December, 1909, contains a dense and vigorous growth of *Anacharis*, also plenty of fresh-water algæ. It stands in the factory room subject to the fall of factory dust, and to the changes of temperature in the room. When the room gets unusually cold the ancyloids mostly retire out of sight, temporarily. December 9, 1909, two specimens with the third stage of the shell partly grown were taken near the top of the jar. A sudden spell of unusually cold weather having begun two nights previous may account for the ancyloids having gone, as they did, into hiding, but it was somewhat surprising that the more nearly mature form had not also hidden.

The 8 × 6-inch Jar.—This had sand on the bottom and was planted with *Anacharis* from the larger jar, carrying with it *Ancylus*, *Gundlachia* and *Planorbis parvus* in the summer of 1908. The following winter, having nothing but sand and water to live on, the vegetation had become rather attenuated and feeble looking. The ancyloids were few and perhaps not more than half as large as those in the larger jar. January 19, 1909, two or three immature septate specimens were taken from this jar, and February 10 one about half grown. Very few ancyloids were seen about this time in this jar. February 11 two immature septate specimens were taken, being all of either form which were at that time visible. February 24, 1909, for the first time since the eleventh, a small ancyloid was noticed. On the twenty-seventh one moderate-sized but fully septate individual was taken and one ancyloid seen. Another septate was taken March 8, and March 11–13 a solitary ancyloid was noticed.

Fearing that there was not enough stock in the jar to

continue the race, March 15, Mr. Allen put in half a dozen ancyloids from the large jar. March 29 a mature septate was taken out, and it was noticed that the *Planorbis* looked frail as if insufficiently supplied with lime salts. October 11, 1909, two half-grown septates were taken from this jar. In the winter (1909–10) the *Planorbis*, for some unknown reason, completely disappeared.

From these data Mr. Allen concludes that about 80 per cent. of the stock in this jar had assumed the septate form, the conditions obviously being such as to stunt both *Anacharis* and ancyloids. In the 15 × 9-inch jar the vegetation is luxuriant and abundant, and the septate individuals produced were only about two to five per cent. of the ancyloids. From this Mr. Allen concludes that the formation of a septum is promoted by causes which tend to restrict or retard growth.

The 9 × 7-inch Jar.—This has a mixture of sand and soil at the bottom. There is plenty of algal growth, but the *Anacharis* is not as vigorous as in the 15 × 9-jar, from which it was stocked with ancyloids and *Planorbis*. In the winter of 1906–07 it yielded two septates. The winter of 1907–08 ancyloids were fairly numerous, more so than during the first winter, but no septates were detected. July 1, 1908, young fry, hatched that season, were visible. March 8, 1908, a fine large mature *Gundlachia* was taken. The original ancyloid part was deep black and the flaring expansion beyond it was colorless and transparent. In the sand-bottomed jar the mature *Gundlachia* is uniformly yellowish translucent, but in the large jar with mud bottom the whole shell gets blackish. December 13, 1909, a census of this jar was attempted. The day was dark and a count difficult, but the result was six septates and two ancyloids, all eight being small and immature.

A Jar without Planorbis.—Thinking it might be desirable to have a stock of the ancyloids not associated with *Planorbis*, Mr. Allen, about February, 1909, when

the *Planorbis* was not breeding, transferred some *Anacharis* and a number of mature ancyloids to a new 15 × 9-inch jar, taking care not to introduce any *Planorbis*. May 3, 1909, the first ancyloid hatched in the jar was noticed; it was about half the size of the parents. Others appeared later. By December, 1909, the parent stock had disappeared and the stock hatched in the jar remains very small, indicating some unfavorable condition. The bottom of the jar was covered with a mixture of ordinary and swamp soil, but the supply of swamp soil used in previous jars having been used up, that in the present jar was taken from another place, and may have contained some unfavorable matter. The *Anacharis* in the jar is fairly flourishing, but there is no green algal growth.

General Conclusions.—The *Gundlachia* may reproduce before assuming the completely mature form. The shell varies in apparent color in accordance with the muddy or sandy character of the bottom soil, but the dark coating in the former case is not incorporated with the shell structure.

The ancyloid stage has a period of least activity in May. In July and August the septates appear. In autumn and early winter the third stage is developed, becoming mature and complete in February or March. This course is, however, not invariable in the aquarium or domesticated specimens, since Mr. Allen has taken ancyloids in January or February, an irregularity probably due to temperature and which might not have occured in specimens under perfectly natural conditions. It is not certain that the ancyloids detected by Mr. Allen in July and August were the young of that season, since the minute creatures are very difficult to detect in the aquarium and can not be handled. They are so translucent in the younger stages as to be practically invisible. However, it is probable that the eggs are laid during the winter and hatched in the very early spring.

It seems likely that under average conditions only a

small proportion of the individuals advance beyond the septate stage; and also that, of the ancyloids, only part reach that stage. It is also probable, from Mr. Allen's observations, that anything which tends to retard development may coincidently increase the tendency to form a septum.

Since there is a period of least activity in May, a natural observation year will be from one May to another. Mr. Allen summarizes the results obtained during the period, May, 1908, to May, 1909, as follows:

None being taken before July nor after the following March, there were secured between July, 1908, and March, 1909, inclusive:

15 × 9-inch jar 4 septates 9 × 7-inch jar 1 septate 8 × 6-inch jar 10 septates	total 15.

From August 19, 1909, to December 13, 1909:

15 × 9-inch jar 8 septates 9 × 7-inch jar 6 septates 8 × 6-inch jar 2 septates	total 16.

Further correspondence, during February, 1910, affords additional notes.

A lot of the wild Thornburg *Ancylus* in alcohol was sent by Mr. Allen and, contrary to his expectation, on careful comparison with his series of ancyloids from his aquaria, no difference, beyond slight individual variations, could be observed in the shells of the two series, while the radula and the soft parts, after repeated comparisons, seemed to be identical in both.

Mr. Allen especially notes that in the winter, 1909–10, the septates were the prevailing form in his aquaria, exactly the reverse of the case when the aquaria were freshly established. The generation, which appeared in May and June, 1909, in the "*Planorbis*-free" jar, was dwarfed was not in sight during the latter part of the winter, 1909–10, and may possibly have all died. Mr. Allen attributes the poor success of this jar to the use of

swamp soil from a different place from that previously used.

February 15, 1910, being a dark day and therefore favorable for the septates to be out of sight, Mr. Allen counted those visible in the large aquarium. Six septates and one ancyloid were noted. This illustrates the observation that (excepting the "*Planorbis*-free" jar) the septate is the prevailing form this season, and is promoted by causes which dwarf or retard growth.

After noting the inexplicable way in which fresh-water mollusks sometimes appear and disappear from pools where they occur, Mr. Allen further suggests that the septate form may be a prelude to total disappearance of the species from a given place.

Another count on February 17, 1910, gave three ancyloids and three septates in sight, which Mr. Allen remarks is the first time for a considerable period that the two forms have appeared in equal numbers. In the large jar every mature specimen seen this season has been conspicuously bicolored, the ancyloid or septate part being stained deep black, while the flaring extension is translucent and colorless, indicating that a resting period intervened between the completion of the septum and the formation of the mature shell.

Three ancyloids seen February 17 were all translucent and about the same size. There can be little doubt that they date from the summer of 1909. Hence, Mr. Allen infers that the blackened original shells of the mature *Gundlachia* date from the season previous.

TABLE FOR JANUARY AND FEBRUARY, 1910

Specimens taken or observed

Date	Gundlachia	Septates	Ancyloids
January 12 (big jar)	1	1	0
January 19 (big jar)	1	0	0
January 31 (small jar)	1	0	0
February 4 (big jar)	2	0	0
February 5 (big jar)	3	1	0
February 6 (medium jar)	0	2	0

My last communication from Mr. Allen, dated December 11, 1910, contains the following additional notes:

As I have already written there was plenty of A-form (ancyloids) and no G-form (septates) visible in my original large jar last summer. But, since the latter part of November, besides ancyloids in various stages, young septates have been visible in fair abundance. I counted about a dozen in sight at one time.

He concludes that ancyloids are present most of the year, but only young ones in May and mostly also in June. But septates appear to be a strictly winter form, that is, the immature septate stage appears in August or later, reaches maturity (*Gundlachia*) in February or March, and disappears about the end of April, after which and a shorter or longer interval the young ancyloids of the season begin to appear in the jars.

If the hypothesis stated at the beginning of this paper be well founded, it would explain why mature *Gundlachias* appear, if at all, usually as a few individuals in any given locality, and their presence can not be counted on, as in the usual case of fresh-water mollusks, and is distinctly a rarity in the temperate regions of the continent, where there are no well-defined wet and dry seasons.

NOTES AND LITERATURE

MIMICRY

In some ways it would be a pity if the theory that mimicry has arisen through the operation of natural selection must be discarded since it is so ingenious in itself and was originated and fostered by such masters of theoretical biology. However, the old order seems to be surely giving place to new, here, as in other phases of the study of evolution. Since Wallace's "Papilionidæ of the Malayan Region" the case of *Papilio polytes* has been a classic. The females of this butterfly are of three sorts: one like the male *polytes*, one like *P. aristolochiæ* and the third like *P. hector*. The two latter species are supposed to be distasteful to insectivorous animals while *P. polytes* is supposed to be edible. The two "models" are numerous in individuals and while "*P. hector* and the *hector* form of *P. polytes* are confined to India and Ceylon, both *P. aristolochiæ* and the *aristolochiæ* form of *P. polytes* have a wider range eastward." The case is complete and has been convincing.

However, Punnett[1] found that in Ceylon

> The following statements may be taken as a fair presentation of the facts:
>
> 1. In the low-country the male form of *polytes* female is at least as numerous as either of the other forms, and may be the most abundant of the three.
>
> 2. In the northeast of the island, in the hector country, the aristolochiæ form *polytes* is nearly as abundant as the hector form, though its model is at any rate exceedingly scarce.
>
> 3. Higher up-country, where *P. hector* is rare or absent and *P. aristolochiæ* is common, the hector form of *polytes* is more abundant than the aristolochiæ form.
>
> It is obvious that these statements are not in harmony with the ideas of those who look to the theory of mimicry for an explanation of the polymorphism that exists among the females of *P. polytes*.

His observations concerning the enemies of butterflies confirm those of other heterodox students, namely: that "as serious enemies of butterflies in the imago state birds may be left out of

[1] "Mimicry in Ceylon Butterflies, with a Suggestion as to the Nature of Polymorphism," *Spolia Zeylanica*, Vol. VII, Part XXV, September, 1910.

account,'' that lizards ''certainly do not appear to exercise that nice discrimination with regard to butterflies which is necessary for the establishment of mimicking forms on the theory of natural selection,'' and that asilids are not averse to preying upon ''distasteful species.''

After pointing out that the resemblances on which the theory was based are far less striking in living, moving specimens than in their expanded museum state, he says

Apart then from the questions whether the resemblances in many cases of mimicry are sufficiently close to be of effective service to the mimic, and whether the action of natural selection can be regarded as sufficiently stringent to have brought these resemblances into being, there are still the following difficulties in the way of the acceptance of the hypothesis of those who look to natural selection as an explanation of polymorphic forms in Lepidoptera:

1. The attribution of selection value to minute variation.
2. The absence of transitional forms.
3. The frequent absence of mimicry in the male sex.
4. The inability to offer an explanation of polymorphism, where the polymorphic forms can not be regarded as mimics of a distasteful species.

Moreover, the hypothesis assumes that minute variations of all sorts can be inherited, a position which at present is lacking in experimental proof.

The gist of the constructive part of his paper is as follows:

Natural selection plays no part in the *formation* of these polymorphic forms, but they are regarded as having arisen by sudden mutation, and series of transitional forms do not exist because such series are not biologically possible. Polymorphic forms may arise and may persist, provided that they are not harmful to the species, and it is possible to look upon their existence as due to the absence of natural selection rather than to the operation of this factor. . . . That polymorphism in a species should so frequently be confined to the female sex has long been remarked upon by those who study these matters, and the explanation most favored is that the female, burdened as she is with the next generation, is more exposed to the action of natural selection and in greater need of some protective adaptation. The weak point of such a view is that it does not explain why the male is not similarly protected. In connection with this problem recent Mendelian research on sex-limited inheritance is highly suggestive. It has been shown that certain types of inheritance receive their simplest explanation on the assumption that the female is heterozygous for a sex factor not contained in the male and that this sex factor may, on segregation of the gametes, repel the factor for some other character for which the female is also

heterozygous. From the beautiful experiments of Doncaster and Raynor it has been inferred that inheritance of this type occurs in the common currant moth (*Abraxis grossulariata*), where a distinct color variety, var. *lacticolor,* occurs. The factor for *grossulariata* pattern appears to segregate against the female sex factor, with the consequence that in only one type of mating, and that a rare one, is the *lacticolor* pattern transmitted to the male sex.

Gametic formulæ are suggested and the conditions they impose are mentioned, but no breeding work was done. Whether the above explanation of the behavior of *grossulariata* is correct or not and also the correctness of the suggested formulæ for *polytes* are immaterial to the present discussion. It is now well known that "mutations" do occur in the females of insects and that the new characters can be transferred to the male by proper breeding. But, why do the mutants of *P. polytes* resemble greatly, even if they do not do so to such an extent as had been supposed, other species? On account of similar anatomical and physiological make up; or, in this case, did the proper gametic couplings once take place so that the then new female type was transferred to the males (as in *grossulariata*) and was thereafter continued with such other modifications as were necessary to separate them taxonomically? In other words, the mimicking species came first and gave rise to the model!

Mutation, in itself, is not the whole story. Granting it, we must be given a reason for the mutant resembling something else and while the amendment just made to Punnett's paper *may* carry for this case, the chances are against it and we can not apply it to resemblances between species of different orders. In this connection, however, there seems to be an important thing which is often overlooked. It would be far more wonderful if, among the thousands of new forms which have arisen, there were no resemblances than it is that some of the forms are very much alike.

As Punnett and others have pointed out, the same process which brought about such a close resemblance between, for example, earwigs (Orthoptera) and rove beetles (Coleoptera) that they are frequently mixed in entomological collections doubtless caused also the resemblances (here called mimicry because an advantage can be imagined) between certain flies and certain stinging Hymenoptera. If "chance" or "environment" is used in the former case it is not unlikely that it applies in the latter also.

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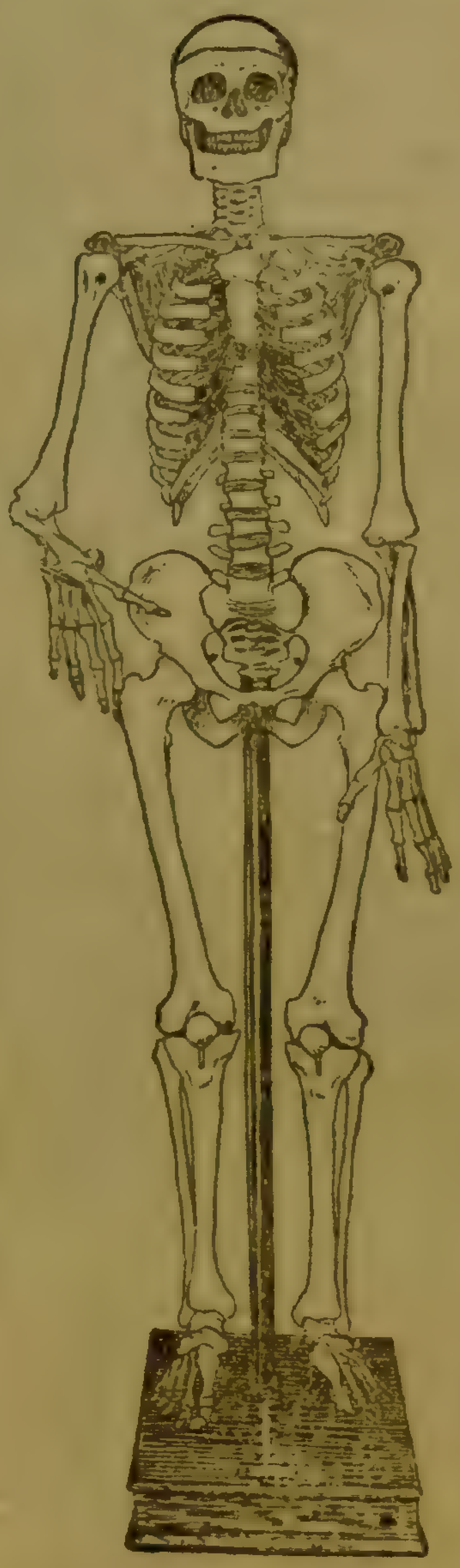

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Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

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GENETICAL STUDIES ON ŒNOTHERA. II

SOME HYBRIDS OF *Œnothera biennis* AND *O. grandiflora* THAT RESEMBLE *O. Lamarckiana*[1]

DR. BRADLEY MOORE DAVIS

THE status of *Œnothera Lamarckiana* is a matter which must be given serious consideration in any attempt to judge the value of De Vries's mutation theory, for the reason that the behavior of this form in throwing off marked variants (mutants) from the type has been regarded by De Vries as direct experimental proof of mutation. Indeed, the theory of De Vries may fairly be said to rest chiefly upon the behavior of this interesting plant, the account of which forms so large a part of his work, "Die Mutationstheorie," 1901–1903.

Aside from his claim of direct proof of the origin of mutations from *Œnothera Lamarckiana*, De Vries offers a considerable body of indirect evidence of the sort presented in Darwin's "Variation of Animals and Plants under Domestication," and in that extensive and very carefully sifted account of Bateson, "Materials for the Study of Variations," 1894. However, much of this indirect evidence of De Vries deals with the origin of "sports" from domesticated forms or with the origin

[1] Contribution from the Laboratory of Genetics, Bussey Institution of Harvard University No. 7. An investigation conducted with aid from the Elizabeth Thompson Science Fund for which the author desires to express his indebtedness.

of new forms under conditions that are not typical of those of nature in the wild. For these reasons such evidence could never appeal with so much force as would direct experimental proof that a wild species is in the habit of producing suddenly new types sufficiently distinct from the parent form to rank as new species or even as strongly marked varieties.

In "Die Mutationstheorie" of De Vries the behavior of *Œnothera Lamarckiana* in giving rise to the so-called mutants is presented as evidence that new species have come into existence without intermediate steps from a form which is assumed to be typical of a species in nature. *Œnothera Lamarckiana* is made to bear the weight of an elaborate hypothesis, treating of fundamental problems, very much as the apex might be made to bear the weight of an inverted pyramid. As the equilibrium of the inverted pyramid depends upon the stability of its apex, so the value for the mutation theory of the evidence from the behavior of *Lamarckiana* must rest with the status of this plant as a form truly representative of a typical species.

De Vries from the beginning took it for granted that *Œnothera Lamarckiana* was a native American species introduced into Europe, an assumption that was perhaps not unnatural, although dangerous when the responsibility of direct proof of the origin of species by mutation was laid upon its behavior. As far as the writer is aware, *O. Lamarckiana*, as a wild American species, is unknown. No American locality can be cited where it may be found as a clear component of the native flora. There are certain records of its presence under conditions that indicate the possibility of its being sometimes a garden escape, and there is some herbarium material, referred to *Lamarckiana*, which, however, has not been tested by culture and was collected at times when the importance of the most critical judgment in identification was not appreciated. It cannot be said that American botanists are not alive to the importance of the status of

Lamarckiana, for it is well known that a certain group would follow with persistence any clue that might give evidence of its being or having been an American native species.

Critics of the evidence for De Vries's mutation theory have been aware of the point of weakness that lay in the uncertain status of *Œnothera Lamarckiana* and the suggestions of Bateson and Saunders ('02, p. 153), East ('07, p. 34), Boulenger ('07, p. 363), Leclerc du Sablon ('10, p. 266), Tower ('10, p. 322), and others have probably occurred to many, namely, that this plant is of hybrid origin and that the appearance of its "mutations" is due to the continued splitting off of variants after the manner of hybrids. This view is held by a number of American botanists with whom the writer is acquainted and represents the attitude of those who are sceptical of the importance of mutation as a factor of organic evolution in nature. If *Lamarckiana* is of hybrid origin it should be possible to obtain evidence of its probable parentage, and the present paper offers a hypothesis with a considerable body of evidence in its favor. After the evidence has been presented the hypothesis will be discussed in the concluding section entitled "The Possible Origin of *Œnothera Lamarckiana* as a Hybrid of *O. biennis* and *O. grandiflora*."

None of the hybrids of *biennis* and *grandiflora* described in the following pages are identical with *Lamarckiana*. There are important differences, chiefly of foliage and stem markings, which distinguish the hybrids at a glance, but on the other hand these characters in taxonomy would be considered of minor importance and the hybrids, if their origin were unknown, could not be placed elsewhere than next to *Lamarckiana*. Furthermore, these differences are of a sort that are likely to be much less apparent when the results of crosses made this summer (1910) between certain types recently differentiated become known in succeeding cultures. In an investigation of this character the results, as every

student of genetics knows, come slowly, and the writer feels no necessity of offering an apology in publishing preliminary data, since they are based on three seasons' study, even though he hopes to present more conclusive evidence in the future.

The cultures of the past season (1910) were grown partly at the Bussey Institution and partly in the Botanic Garden of Harvard University, where facilities were offered for which the writer is deeply indebted.

METHODS

To break the biennial habit and obtain flowering plants in one season it is only necessary to sow seeds in the hot house during the winter, where rosettes will develop, which may be set out in the open in the early spring. The cultures of 1910 were sown early in January and had developed large rosettes by May 5, when the plants were transferred to the gardens. It is best to sow the seeds thinly in large seed pans (with, of course, sterilized soil) from which each individual seedling may be potted.

Cross pollination was always performed on flowers from which the unopened anthers had been removed. The best results are generally obtained when a castrated flower is left bagged for twelve to twenty-four hours before the pollen is applied, in order that the stigma may have time to mature fully which will be evident from the moist exudation on its surface. Strong manila bags tied firmly over the pollinated flowers have proved more satisfactory than special bags of paraffin paper, which appear to hold the flowers in an atmosphere too moist for the best results. It is my practise to dip the forceps in a bottle of alcohol before each transfer of pollen and also to rinse the hands in alcohol. The pollen of *Œnothera* is so sticky that under ordinary conditions there is no danger from wind blown pollen, and by following the practise outlined above there is little or no probability of impure pollination.

In the future my plan will be to sow the seed capsule

by capsule, which is the safest method to obtain quantitative results. In the past I have sown from bulk collections of seed and my studies so far must be regarded as primarily qualitative in character. This practise was followed under the impression that probably only a small proportion of the seed from a cross, apparently as extreme as that between *biennis* and *grandiflora*, would germinate. The results, however, have shown that the seed of this cross is fertile to a very high degree. In consequence my cultures of this season gave three or four times more seedlings than it was practicable to bring to maturity. A process of selection became at once necessary, which was followed with the end in view of obtaining a variety of types, but it soon became evident, with the later development of the cultures, that it is impossible to select with accuracy among the young seedlings. Thus plants which showed certain tendencies as young rosettes or seedlings of five to nine leaves often changed very materially in later growth. For these reasons my cultures of this year even as qualitative studies are undoubtedly not fully representative.

Œnothera biennis L.

My first crosses between *biennis* and *grandiflora* were made at Woods Hole, Mass., in 1908. This locality was carefully searched for rosettes of *biennis* with broad leaves and two plants of this character were transplanted from waste ground to the garden. The rosettes were similar and at maturity the plants proved to be the same form of *biennis* and were practically indistinguishable. These two plants were the starting points of two strains of *biennis*, designated A and B, which have been cultivated through two and three generations, respectively, and have proved constant.

It seems quite certain that under the name *Œnothera biennis* is included a number of races with well-marked peculiarities. These races are probably very pure, for the reason that close pollination is certainly usual, if

FIG. 1. Mature rosette of *Œnothera biennis*, B (10.21a).

not universal, among the forms of the species. The lower portions of the stigma lobes in the bud lie below the tips of the anthers which discharge their pollen before the bud opens. As a result the stigma is not only well pollinated in the bud, but cytological studies on my strains A and B have shown that the pollen tubes reach the embryo sacs before there is any opportunity for cross pollination. Hybridization in nature could hardly occur in these forms unless their own pollen should be insufficient for the number of ovules in the ovary or was much slower than foreign pollen in effecting fertilization; alternatives that are very unlikely. These conditions, similar physiologically to those of cleistogamous flowers, are present in all of the forms of *biennis* known to the writer, and have been noted by De Vries for the European types. As a result a strain once established is certain to remain pure throughout at least the great mass of its seeds.

The chief characteristics of the *biennis* strains A and

FIG. 2. Mature plant of *Œnothera biennis*, B (10.21a).

B, employed in the hybrid studies of the present paper, when under good cultivation are as follows:

1. *Rosettes.*—The mature rosettes (Fig. 1), from 3 to 4 dm. broad, have about 40 closely clustered leaves, spatulate, irregularly toothed at their base, and green except for occasional reddish spots. The rosettes are persistent and conspicuous during the early development of the main stem.

2. *Mature Plants.*—The mature plants, 1–1.5 m. high, have a spreading habit (Fig. 2) with long side branches. Stems chiefly green (brownish below), the papillate glands at the base of long hairs also green. Basal leaves on the main stem narrowly elliptical, about 16 cm. long (Fig. 3), leaves above lanceolate.

3. *Inflorescence.*—Bracts lanceolate, less than half the length of the buds (Fig. 4).

4. *Buds.*—About 5.5 cm. long, the cone 4-angled (Fig. 4). Sepals clear green, their tips not markedly attenuate.

5. *Flowers.*—Small (Figs. 3 and 5). Petals about 1.3 cm. long. Lower halves of stigma lobes (when closed) below the tips of the anthers.

6. *Capsules.*—Gradually narrowing from the base, 2–2.5 cm. long.

7. *Seeds.*—Light brown. Those developed in the ovary of *biennis* after pollination by *grandiflora* are similar to the female parent.

FIG. 3. Flowering side branch of *Œnothera biennis*, B (10.21a), with a leaf from lower portion of main stem.

The most striking peculiarities of strains A and B in comparison with certain other American types of *biennis* are:—the small flowers, green stems, and the absence of that red coloration in the papillate glands which is seen in some forms of the species and is conspicuous in *La-marckiana.*

Since differentiating the strains A and B in 1908, I have had an opportunity of observing somewhat extensively various forms of *biennis* in the vicinity of Boston, where the prevailing type has larger flowers, frequently a broader leaf, and usually stems punctate with red tinted glands. There is considerable variation in the characters above mentioned and I have this year selected certain plants growing wild on the grounds of the Bussey Institution that in some respects are likely to prove much more satisfactory for my purposes than the strains A and B. These

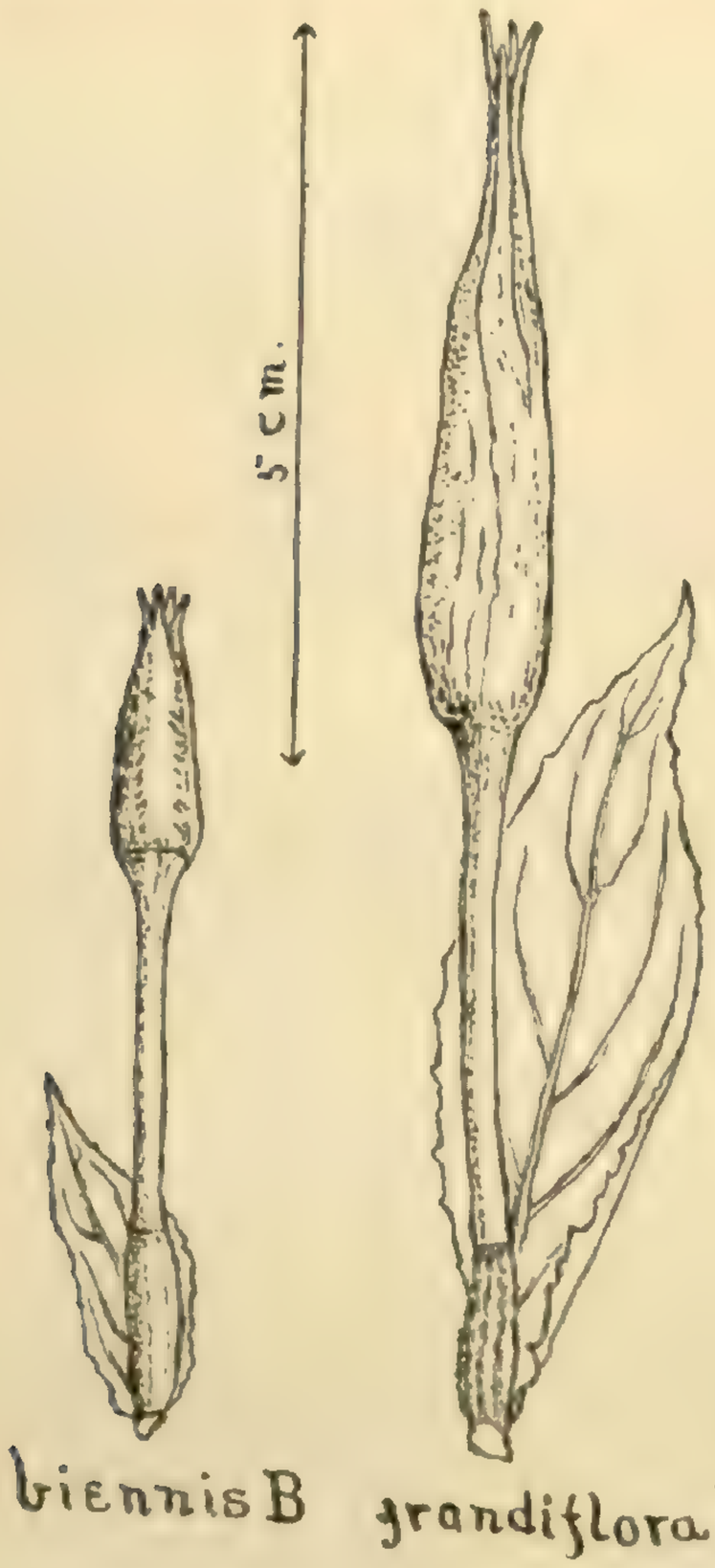

FIG. 4. Buds of *biennis* B and *grandiflora* B.

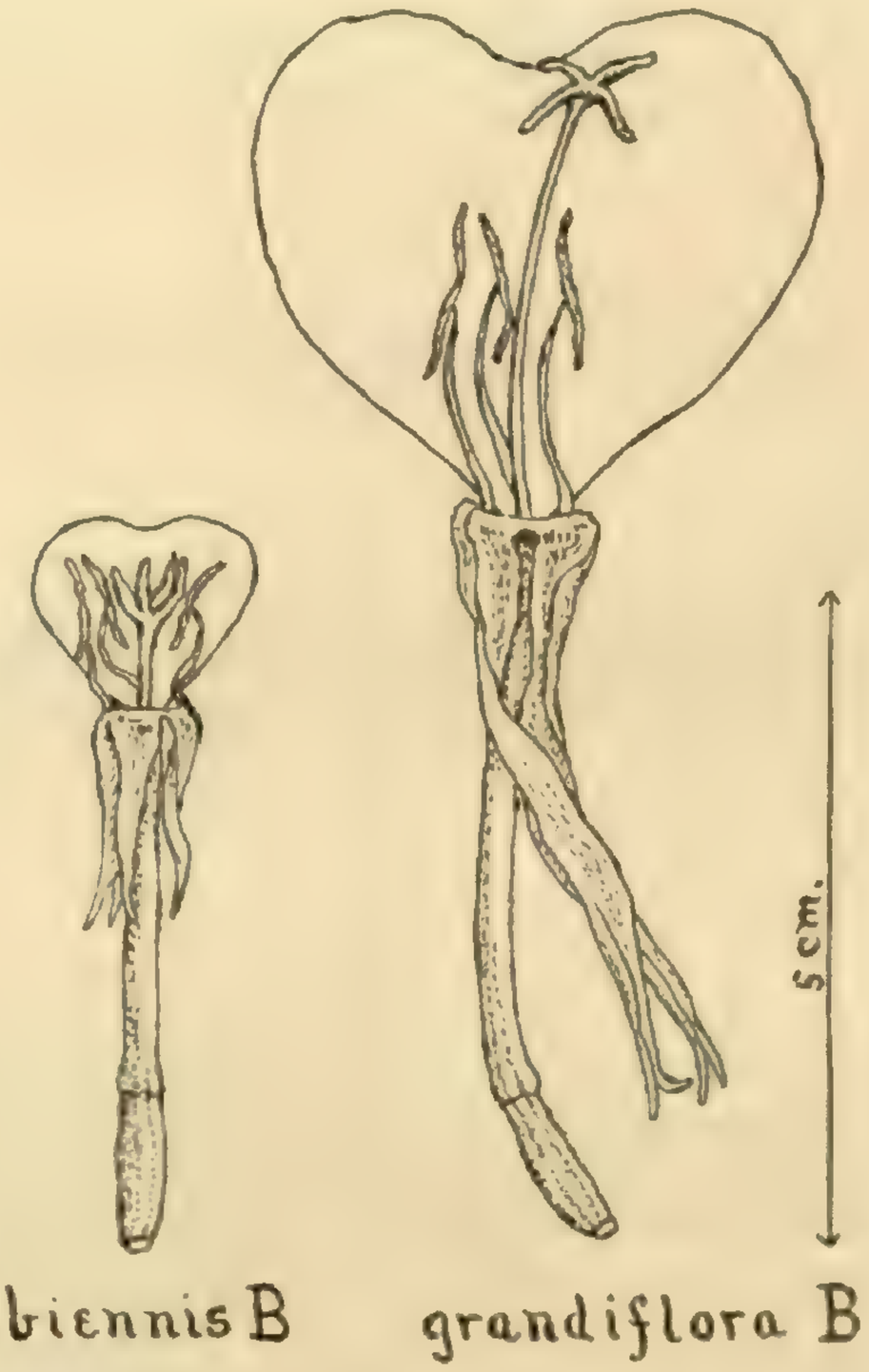

FIG. 5. Flowers of *biennis* B and *grandiflora* B.

plants (strains C and D) have been crossed this year with the best strains of *grandiflora* (B and D) and I expect to grow the hybrids in another season, when the strains will also be tested for their stability. The testing for purity is of course a necessary precaution, although, as explained above, the habit of self-pollination in *biennis* makes it very unlikely that any of these plants are tainted with foreign blood. These strains will not be further described until the prospective cultures have been grown.

Sowings from the wild seed collected as *Œnothera grandiflora*, described below, have given several plants of a southern form of *biennis* (strain S) which may prove of considerable interest since some of its characters (stem coloration, form of buds, size of flowers, etc.) are

very favorable for combination with *grandiflora* with certain ends in view. This southern strain was crossed this season with *grandiflora*, and the hybrids and the parent *biennis* will be studied through further cultures.

Œnothera grandiflora Ait.

We are indebted to Dr. MacDougal ('05, p. 7) and to Miss Vail ('05, p. 9) for accounts of the rediscovery of this remarkable species of the southern United States and for a clear analysis of its probable history. Aiton's original description (1789), from material grown at Kew, states that *Œnothera grandiflora* was introduced by John Fothergill, M.D., in 1778. An expedition of William Bartram in 1776, undertaken at the request of Dr. Fothergill for the purposes of botanical discovery, records the finding of a large-flowered *Œnothera* near Tensaw (Taensa), Ala. Bartram's picturesque and excellent description of this new plant (see MacDougal, '05, p. 7), together with a herbarium specimen in the British Museum from "Hort. Fothergill, 1778," makes it evident that Bartram must have sent seed to Fothergill, through whom the plant was introduced into England in 1778.

Professor S. M. Tracy in 1904 visited the original locality and found the species growing in considerable quantity along the east bank of the Alabama river in the vicinity of Dixie Landing, which is only a few miles from Tensaw. His material agrees with the descriptions of Bartram and Aiton and, according to Miss Vail, with the herbarium specimen of Fothergill, and there seems to be no doubt that *Œnothera grandiflora*, so widely cultivated, has been rediscovered growing wild in its original locality.

My seed of *Œnothera grandiflora* was collected by Professor Tracy at Dixie Landing in September, 1907. During the past three seasons I have sampled the collection to the extent of bringing to maturity from the wild seed thirty-four plants, and in addition some seventy rosettes and young plants have passed under my

inspection. Besides the above I have selected and cultivated from this material three strains (*grandiflora* A, B, and D), which have been carried through a second generation represented by twenty-four mature plants.

It became apparent, as my cultures progressed, that the *Œnothera grandiflora* growing near Tensaw is far from uniform in character. I have so far selected four distinct types of plants, only one of which, however, has been cultivated in later generations. The fact that the stigma of *grandiflora* is generally well above the tips of the anthers prevents pollination in the bud and in the opening flower, and offers a very much greater opportunity for cross pollination than is possible in *biennis*. This condition is probably responsible for the heterogeneity of the species.

The type which I have under cultivation and which has proved stable is characterized by a somewhat broader leaf than is common to the species. From it have been differentiated the following three strains (A, B, and D), which have been used in the crosses with *Œnothera biennis*.

1. Strain D came directly from a wild plant.

2. Strains A and B are the result of a cross between D and a similar plant, F, in the garden at Woods Hole in 1908. The cross was made to fix thoroughly the characters of a broad leaf and red coloration of sepals present in both parents. The two strains (A and B) are essentially similar, differing chiefly in the degree of red coloration present in the sepals, a character that is variable and probably cannot be depended upon as a fixed factor. As a matter of fact, strain D in a second generation has proved very uniform and it is not likely that I shall make further use of strains A and B. All three strains are representative of the larger proportion of the plants of *grandiflora* that have passed under my observation, being, however, what a gardener would select as luxuriant forms with broader and larger leaves than the average.

FIG. 6. Mature rosette of *Œnothera grandiflora*, B (10.4a).

In addition to the type represented by the strains A, B, and D (which is described in the paragraph below) there have appeared in the cultures from the wild seed the following three types markedly different from one another and from the general run of wild *grandifloras*.

1. A type represented by a large plant (2 m. high) peculiar for its light green broadly elliptical leaves, generally green stem, green sepals, and a close rosette of crinkled leaves strongly resembling a half-grown rosette of *Lamarckiana*. This type, represented by a single plant (*grandiflora* I) appeared this year, 1910, and is likely to prove of great interest. It will not, however, be described until its behavior in later generations has been noted and its crosses with *biennis* have been grown.

2. A type represented by a relatively small plant (1.2 m. high) with stiff, broadly lanceolate, revolute leaves, and sepals deeply blotched with red. This peculiar form

FIG. 7. Mature plant of *Œnothera grandiflora,* B (10.4c).

(*grandiflora* R) is too far from the general type of *grandiflora* to be of value in the present study.

3. A type represented by a plant (*grandiflora* Z) with narrow lanceolate leaves, much too narrow to give results, if crossed with *biennis,* that would approach *Lamarckiana.*

The chief characteristics of the *grandiflora* strains A, B, and D, employed in the hybrid studies of the present paper, when under good cultivation are as follows:

1. *Rosettes.*—The mature rosettes (Fig. 6), 2–2.5 dm. broad, have about 20 loosely clustered leaves, broadly elliptical, irregularly and sometimes deeply cut at the base, slightly crinkled, and mottled with reddish brown blotches. The rosettes are transitory, the leaves withering during the development of the main stem.

FIG. 8. Flowering side branch of *Œnothera grandiflora*, B (10.4a), with a leaf from the lower portion of the main stem.

2. *Mature Plants.*—The mature plants (Fig. 7), 1.5–2 m. high, have a more upright habit than *biennis*. Frequently the branching is profuse, the main stem and long side branches being covered with short shoots. Stems reddish, green only towards their tips, the papillate glands following the color of the stem. Basal leaves on the main stem ovate or broadly elliptical, about 15 cm. long (Fig. 8); leaves above broadly lanceolate.

3. *Inflorescence.*—Bracts early in the season leaf-like and more than half the length of the buds (Fig. 4); later becoming very much smaller.

FIG. 9. Rosette of a hybrid (10.30 La), *grandiflora* B × *biennis* A, F_1 generation.

4. *Buds.*—From 9–10 cm. long, the cone scarcely angled (Fig. 4). Sepals marked with reddish brown blotches, sometimes dull and faint; their tips attenuate.

5. *Flowers.*—Large (Figs. 5 and 8). Petals about 3.3 cm. long. Stigma lobes generally 2–5 mm. above the tips of the anthers.

6. *Capsules.*—Tapering rather sharply from the large base, 2.5–3 cm. long.

7. *Seeds.*—Dark brown. Those developed in the ovary of *grandiflora*, after pollination by *biennis*, have the same color as the female parent.

The above description is so worded as to emphasize the characters of the *grandiflora* strains A, B, and D in contrast to the *biennis* strains A and B. It should be compared with the description of the latter forms to understand clearly the conditions that appear in the hybrids, which will now be described.

FIG. 10. Mature plant of a hybrid (10.30 La), *grandiflora* B × *biennis* A, F_1 generation.

HYBRIDS IN THE F_1 GENERATION

The cultures of 1910 in the F_1 generation were hybrids of three different combinations of parents, as follows:

1. *grandiflora* B × *biennis* A (10.30), grown at the Bussey Institution.

2. *grandiflora* B × *biennis* B (10.18) and the reciprocal cross (10.19), grown at the Bussey Institution.

3. *grandiflora* A × *biennis* B (10.17) and its reciprocal cross (10.20), grown at the Botanic Garden of Harvard University.

Bearing in mind that the *biennis* strains A and B are practically indistinguishable and that the *grandiflora* strains A and B are essentially similar, the cultures as a whole would not be expected to differ markedly, which was the case.

The figures of hybrids published with this paper are from two plants in the first culture (*grandiflora* B ×

FIG. 11. Flowering side branch of a hybrid (10.30 La), *grandiflora* B x *biennis* A. F_1 generation. At the left is a leaf from the lower portion of the main stem.

biennis A). They were selected as likely to prove the most interesting for further cultures in the F_2 and later generations. These two plants 10.30 La and 10.30 Lb will be described in some detail, together with the general features of the cultures.

1. *grandiflora* B $\times$ *biennis* A (10.30). This culture gave about 400 seedlings from which 57 were selected for the breadth of the cotyledons and the shortness of their petioles. These were brought to maturity. The characters of the parents were blended in the rosettes which had long, broadly elliptical leaves, toothed below, and col-

FIG. 12. Rosette of a hybrid (10.30 Lb), *grandiflora* B × *biennis* A, F_1 generation.

ored with large reddish spots and blotches. The mature plants likewise presented the characters of both parents blended in the habit, foliage, and flowers, all the characteristics of form and measurements being clearly intermediate. It was possible to distinguish certain rosettes as being more *biennis*-like or more *grandiflora*-like than the culture in general and the mature plants from these rosettes also exhibited similar differences. The plants of the culture therefore presented a certain range, the extremes being readily distinguished as more like one parent than the other although never approaching closely to either. Between the extremes were numerous transitions.

Two rosettes of this culture were selected for their resemblance in certain particulars to *Œnothera Lamarckiana* and the mature plants from these proved to be among the most interesting in the gardens. These hybrids, 10.30 La and 10.30 Lb, were representative of a

FIG. 13. Mature plant of a hybrid (10.30 Lb), *grandiflora* B × *biennis* A, F_1 generation.

type of hybrid of *biennis* and *grandiflora* that has proved not uncommon in my cultures. The description of these two plants will now follow, arranged to bring out the salient features in comparison with the parent species and with *Lamarckiana*.

Hybrid 10.30 La. 1. *Rosette*.—The mature rosette (Fig. 9), about 3.3 dm. broad, was persistent. Older leaves more elliptical and less spatulate than those of *biennis* (Fig. 1), deeply cut at the base as in *grandiflora* (Fig. 6), spotted with red. The younger leaves were markedly crinkled as in *Lamarckiana* (Fig. 15), but narrower and more pointed.

2. *Mature Plant*.—The mature plant (Fig. 10), 1.8 m. high, had a straggling habit with long branches arising from the base, short clustered shoots above (*grandiflora*-like), a habit very different from the symmetry of *La-*

FIG. 14. Flowering side branch of a hybrid (10.30 Lb), *grandiflora* B × *biennis* A, F_1 generation. At the left is a leaf from the lower portion of the main stem.

marckiana (Fig. 16). Stem green above, mottled red below, occasional regions where red-tinted papillate glands lay on green portions of the stem as in *Lamarckiana*. Basal leaves on the main stem (Fig. 11) elliptical, about 22 cm. long, only slightly crinkled and not so long as the much-crinkled basal leaves of *Lamarckiana* (Fig. 17). Leaves on the upper portion of the plant broadly elliptical, slightly larger than those of *Lamarckiana*.

3. *Inflorescence*.—The inflorescence (Fig. 11) was strikingly similar to that of *Lamarckiana* (Fig. 17), the bracts being of about the same size and shape.

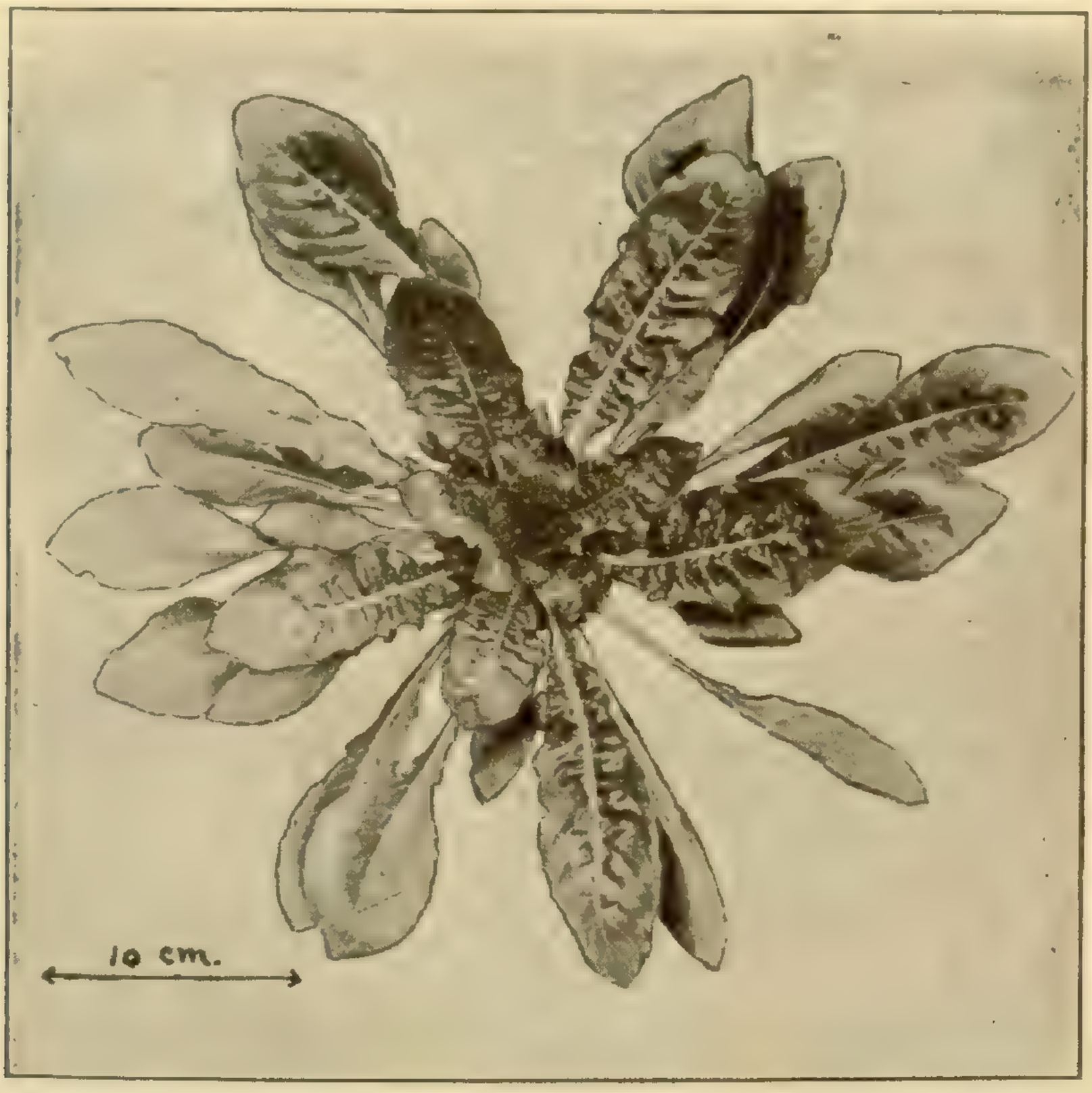

FIG. 15. Rosette of *Œnothera Lamarckiana* (10.23c).

4. *Buds.*—From 6 to 6.5 cm. long, about the same size as *Lamarckiana* and similar in form (compare Fig. 11 with Fig. 17), sepals green. Intermediate in size between those of parents.

5. *Flowers.*—Scarcely distinguishable from those of *Lamarckiana* (compare Fig. 11 with Fig. 17) and with the form and proportions of the parents blended. Petals about 2.2 cm. long. Base of stigma lobes slightly below the tips of the anthers.

6. *Capsules.*—About 2.3 cm. long, intermediate in size between those of the parents.

7. *Seeds.*—A shade of color clearly intermediate between the light and dark brown of the parents.

Hybrid 10.30 Lb. 1. *Rosette.*—The mature rosette (Fig. 12), about 3 dm. broad, was persistent. Older leaves much broader than those of *biennis* (Fig. 1), cut at the base as in *grandiflora* (Fig. 6), a lighter green than the average of the culture, and with relatively few red spots as in *Lamarckiana.* The younger leaves were

FIG. 16. Mature plant of *Œnothera Lamarckiana* (10.23c).

strongly crinkled, almost as broad as those of *Lamarckiana* (Fig. 15), but more pointed.

2. *Mature Plant.*—The mature plant (Fig. 13), 1.7 m. high, with long branches from the base, had a habit more spreading than that of *Lamarckiana* (Fig. 16), but was otherwise very similar. Stems green above, mottled red and brown below, the papillate glands of the same color as the portions of the stem upon which they lay. Basal leaves on the main stem (Fig. 14) broadly elliptical, about 20 cm. long, without crinkles and not so long as the

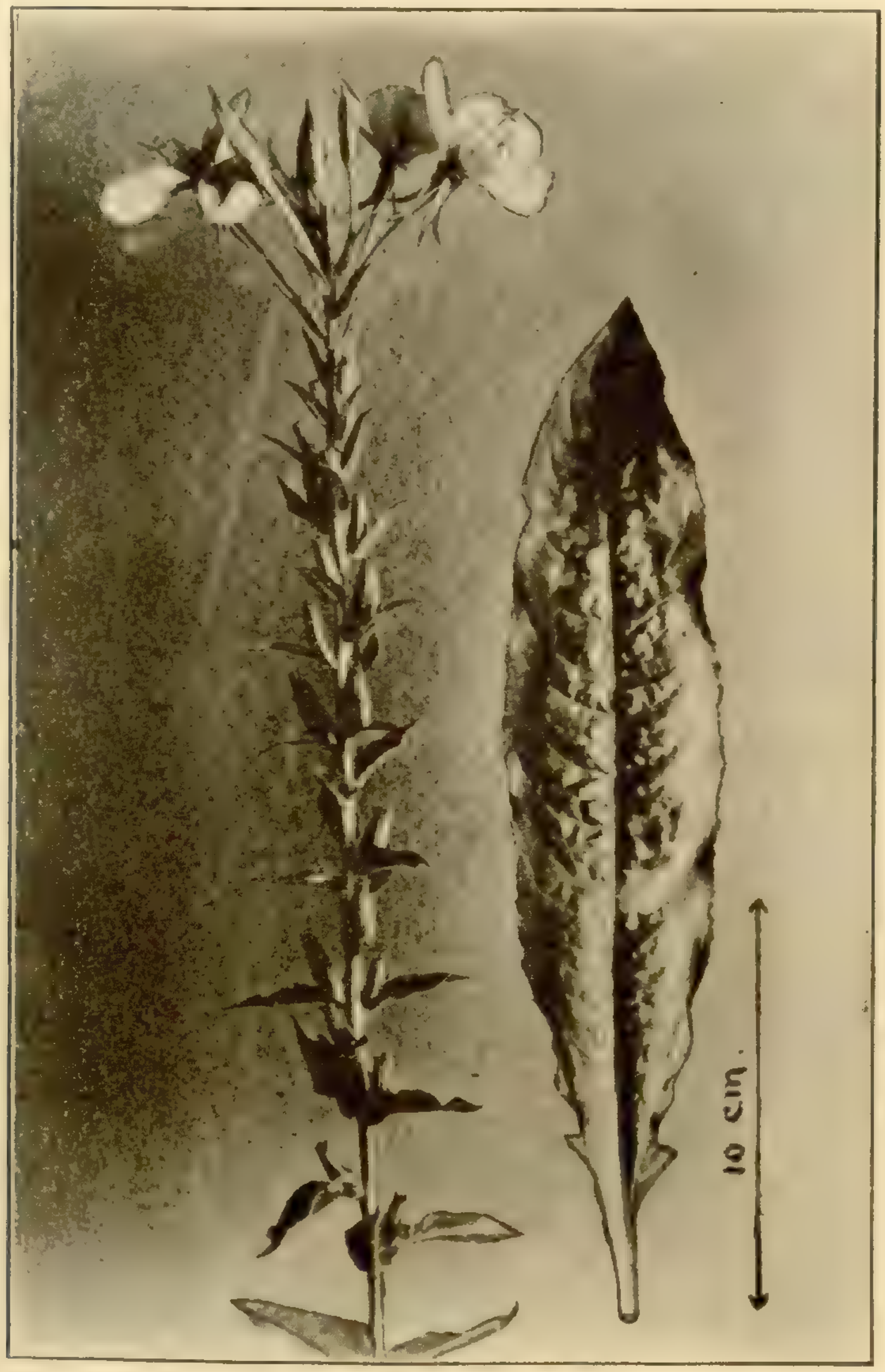

FIG. 17. Flowering side branch of *Œnothera Lamarckiana* (10.23zb), with a leaf from the lower portion of the main stem.

much crinkled basal leaves of *Lamarckiana* (Fig. 17). Leaves on the upper portion of the plant broadly elliptical, slightly crinkled, similar to those of *Lamarckiana*.

3. *Inflorescence*.—The inflorescence (Fig. 14) had bracts longer than those of *Lamarckiana* (Fig. 17), somewhat crinkled and similar to the bracts in figures of *Œnothera scintillans* (De Vries's "mutant" from *Lamarckiana*).

4. *Buds*.—From 6–6.5 cm. long, about the same size as those of *Lamarckiana*, but with a more pointed cone and attenuated sepal tips (contrasted in Fig. 18), sepals green. Intermediate in size between those of the parents.

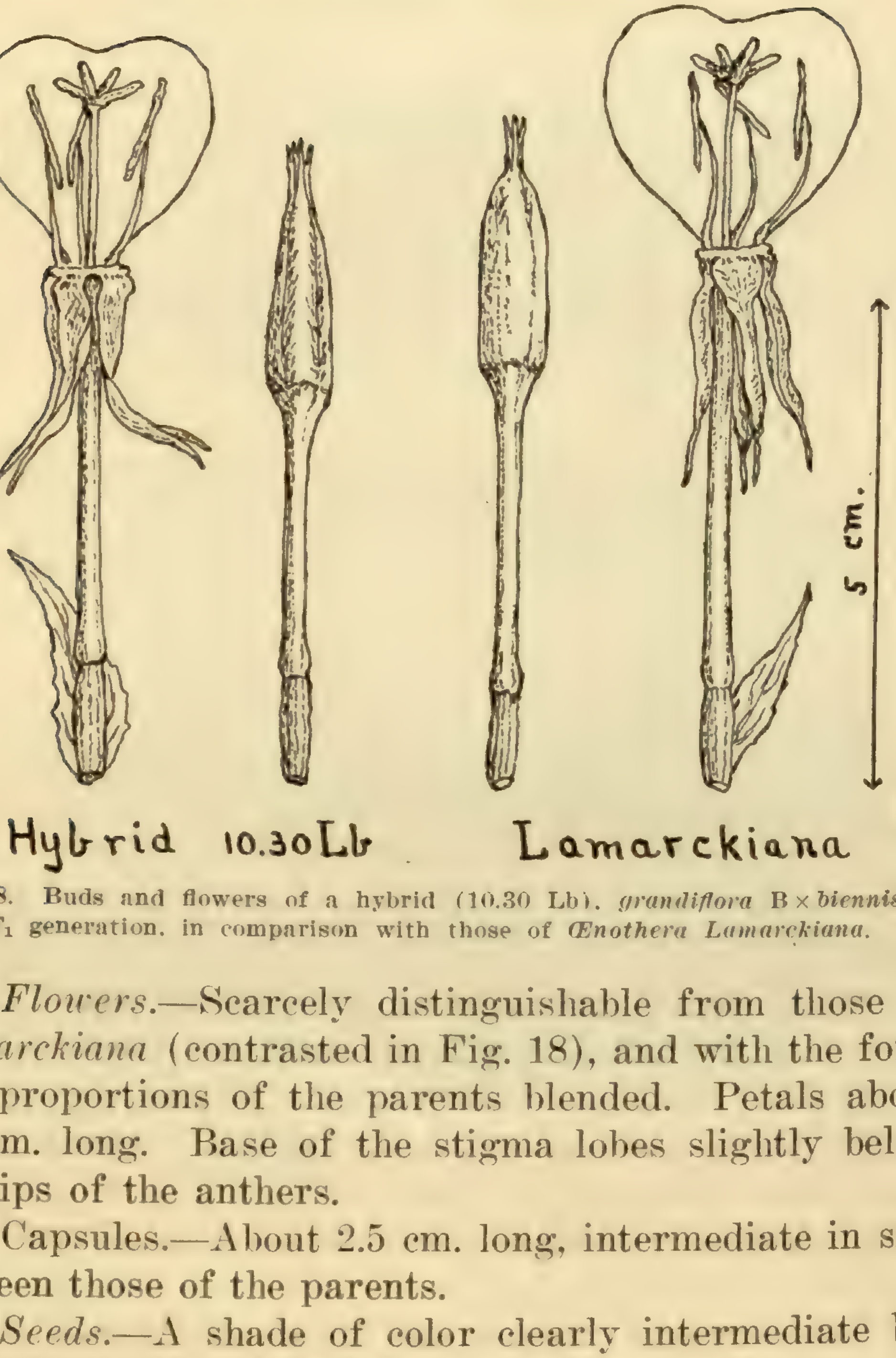

FIG. 18. Buds and flowers of a hybrid (10.30 Lb), *grandiflora* B × *biennis* A, F_1 generation, in comparison with those of *Œnothera Lamarckiana*.

5. *Flowers.*—Scarcely distinguishable from those of *Lamarckiana* (contrasted in Fig. 18), and with the form and proportions of the parents blended. Petals about 2.2 cm. long. Base of the stigma lobes slightly below the tips of the anthers.

6. Capsules.—About 2.5 cm. long, intermediate in size between those of the parents.

7. *Seeds.*—A shade of color clearly intermediate between the light and dark brown of the parents.

An examination of these two hybrid plants with respect to the contributions by their respective parents may be readily made by comparing the illustrations and descriptions of rosettes, mature plants, inflorescence, and flowers, bearing in mind that the parent *biennis* A is essentially indistinguishable from the strain *biennis* B which is here figured. It will be found that the hybrids present the characters of the parents in a blend. By a blend it must

not be inferred that the characters of the hybrids are a perfect mean as to the measurement and proportions of their organs. This is certainly not the case for all of the characters of the hybrids and it would be a difficult matter to determine a perfect blend for a single character because of the fluctuating variations in the parent strains. All that I desire to demonstrate in the present account is the fact of blended conditions throughout these hybrids of the first generation, and the total absence of clear dominance of one parent over the other with respect to any character.

It would be very difficult and probably impossible to support satisfactorily a claim that either of the two parent plants exhibited its influence to a measurably greater degree than the other. To illustrate this point let us examine hybrid 10.30 La. The rosette (Fig. 9) of this plant might be said to be more like that of *biennis* than of *grandiflora*, but the habit of the mature plant (Fig. 10) with respect to its short clustered shoots is more like the latter parent than the former, and thus two characteristic stages of the plant suggest opposite conclusions. This general balance of the influence of one parent over the other was manifest throughout the greater part of the culture, but, as previously noted, a small proportion of the hybrids was readily distinguishable as being more like *biennis* or *grandiflora* although never approaching closely to either parent form.

The chief points of resemblance between the two hybrid plants just described and *Œnothera Lamarckiana* may be briefly summarized as follows:

1. The inflorescence was very similar to *Lamarckiana*, especially in the case of hybrid 10.30 La from which many branches might have been picked that as herbarium specimens could not have been separated from a mixed and varied collection of *Lamarckiana* branches similarly prepared.

2. The only essential difference between the buds lay

in the slightly greater attenuation of the sepal tips especially in the case of the hybrid 10.30 Lb.

3. The flowers of the hybrids were scarcely distinguishable from those of *Lamarckiana*, the small differences in the measurement of parts being no greater than might be expected in any reasonably large and varied culture of *Lamarckiana*. The chief difference with respect to the flower lay in the clear green color of the ovaries of the hybrids, the glands of which were not tinted red, as is characteristic of all material of *Lamarckiana* that the writer has seen.

4. Although the capsules were somewhat longer and more pointed than in the forms of *Lamarckiana* grown by the writer, they were not so long as in certain "long-fruited races" described by De Vries, who states that the fruits of *Lamarckiana* are highly variable and figures capsules as pointed as those of my hybrids (De Vries '09, p. 528, et seq., Fig. 114).

The points of difference concern chiefly the vegetative portions of the plants under discussion.

1. The rosette of the hybrids consisted of mixed forms of leaves, only the younger resembling the markedly crinkled leaves of *Lamarckiana*.

2. The habit of the mature hybrid plants was more straggling, lacking the symmetry characteristic of *Lamarckiana*. The basal leaves were not so large and were but slightly crinkled; the upper leaves, especially in the case of hybrid 10.30 Lb, were similar to *Lamarckiana*.

3. The coloration of the stem was green above and mottled red and brown below, in contrast to the green stems of *Lamarckiana* punctate with red-tinted papillate glands. Similar glands were present in the hybrids, but their color (portions of 10.30 La excepted) was that of the regions of the stem upon which they lay.

The hybrids, therefore, resembled *Lamarckiana* as to the inflorescence, floral parts, and fruits; they differed chiefly in certain vegetative characters and in the coloration of the stem. It remains to be seen through further

cultures which of the two, the resemblances or the differences, are more stable in inheritance and variation.

The type of *Lamarckiana* which has been compared in this paper with the hybrids of *biennis* and *grandiflora* is one with which I have been familiar for the past five years. It has been represented in my cultures by strains from seed that has come to me through three different sources, all of the seed, however, originally being derived from the cultures of De Vries. These strains have not differed materially from one another, and as grown in my small cultures have not exhibited marked variation. The rosettes and mature plants have agreed in habit and foliage with the descriptions of *Lamarckiana* in "Die Mutationstheorie." The flowers have, however, been uniformly smaller than the measurements and figures of De Vries, the petals being about 2.5 cm. long instead of measuring 3 cm. or more. In the flower structure the position of the stigma has proved more variable than one would be led to suppose by the figures and descriptions of *Lamarckiana*, the stigma generally being but slightly above the tips of the anthers or about at their level, and in some plants distinctly below.

2. *grandiflora* B × *biennis* B (10.18), and the reciprocal cross (10.19). From about 200 seedlings of the first culture and about 250 seedlings of the second culture, 66 and 70 plants, respectively, were brought to maturity, being selected for the breadth of the cotyledon and the shortness of its petiole. As the rosettes formed there appeared much variation in the amount of anthocyan developed in the leaves, the larger proportion being marked with dull red spots and blotches, only a small number having few spots as in *Lamarckiana*. The form of the leaves likewise varied and certain of the rosettes were readily separated as being more *biennis*-like or *grandiflora*-like than the average. The plants that developed from these extreme forms of rosettes were also somewhat more like the respective parents than the mass of the culture which presented the characters of

the parents thoroughly blended in the form and proportions of habit, foliage, and flowers. Considering the cultures as a whole, there seemed to be no marked difference between the first cross and its reciprocal.

The average types of hybrids in both crosses were essentially similar and a number of types were very close to the hybrids 10.30 La and 10.30 Lb of the previously described culture. Six plants in culture 10.19 were selected for special peculiarities, but these will not be described unless their behavior in the F_2 generation should justify a detailed account.

3. *grandiflora* A × *biennis* B (10.17), and the reciprocal cross (10.20). From about 200 seedlings of the first culture and about 150 seedlings of the second culture, 49 and 60 plants, respectively, were brought to maturity, being selected for the breadth of the cotyledon and shortness of its petiole. These cultures were grown in a stiff clay at the Botanic Garden and presented an interesting contrast to the cultures previously described which were grown in a somewhat sandy well-fertilized soil. The plants were smaller and less vigorous vegetatively, although they flowered very freely. The rosettes and mature plants presented the characteristics of the parents well blended as in the other cultures. There were also a few extreme types that resembled one or the other of the parents more closely than the average. There appeared to be no significant differences between the first cross and its reciprocal. Two plants with marked peculiarities were selected from culture 10.17 and will be carried through an F_2 generation; they will be described if their further cultivation proves of interest.

Although the evidence, not being quantitative in character, is incomplete, nevertheless the following points may be noted, at least provisionally, from these observations on F_1 generations. (1) There was no indication from these cultures of a marked preponderance of either paternal or maternal influence upon the hybrids.

(2) No character of either parent was observed to be dominant. (3) It is doubtful whether there would be any material difference between a cross and its reciprocal if each were equally vigorous. (4) Although the extreme types in the culture, approaching somewhat the respective parents, could be readily distinguished, they were connected by transitional forms and a sharp line could not be drawn between two sets of hybrids, such as have been described by De Vries ('07, '08) as "twin hybrids" and reported for crosses between the *Onagra* group and *Lamarckiana*. From observations on small cultures during the season of 1909 (Davis '10, p. 113) the writer was led to believe that "twin hybrids" might be present in this cross, but he no longer regards this as probable.

Hybrids in the F_2 Generation

In a recent paper (Davis '10) I described two small cultures of hybrids between *biennis* B and *grandiflora* D that were grown at the Botanic Garden of Harvard University in the season of 1909. Four of the plants of these cultures were of special interest as presenting flowers and inflorescences very similar to *Lamarckiana*, although differing markedly in foliage. I unfortunately was unable to observe the early development of these plants and for this reason they were not very good forms on which to base studies of their progeny in the F_2 generation. Their seed was, however, sown this season and the cultures, described below, were of interest as indicating the probable behavior of hybrid plants of *biennis* and *grandiflora*. These four lines will not be cultivated further, since I have in the hybrids 10.30 La and 10.30 Lb material better suited to the purposes of a quantitative study for the reason that the records of their life history have been kept in detail. The seeds of these hybrids proved fertile to a very high degree, but it was practicable to grow only a small proportion of the seedlings to maturity.

1. Progeny from hybrid 9ba, *biennis* B × *grandiflora*

D. This hybrid plant (Davis, '10, pp. 112 and 113), an excellent blend of the parent forms, was similar to *Lamarckiana* in habit and floral structure, but differed in having smaller, uncrinkled leaves on the lower portions of the plant and larger bracts upon the inflorescence.

From about 600 seedlings 73 plants were carried through the rosette stage and set in the ground, being selected to represent various types. The seedlings were strikingly diverse, some having long cotyledons similar to those of *grandiflora*, others having shorter and broader ones, and a large proportion with small light yellow, etiolated cotyledons. Many of the latter seedlings died before the appearance of the second leaf, the others developed very slowly, forming rosettes one-fourth or one-third the size of the normal with more or less etiolated leaves. Twenty-three of the dwarf rosettes were set out in the garden and of these seven finally grew to be large plants similar to the average of the culture, but with a somewhat etiolated foliage; of the remainder several died and the others developed into dwarf plants from 2–8 dm. high, small leaved, sparsely branched, and with flowers smaller than the average but larger than the *biennis* parent. The behavior of these etiolated dwarfs resembled De Vries's account of the appearance of the form *albida* in his cultures of *Lamarckiana*.

As the normal rosettes approached maturity it was possible to distinguish certain ones as somewhat more *biennis*-like or more *grandiflora*-like than the average, and the mature plants which developed from these showed similar points of resemblance to the respective parents of the cross. Nevertheless, the culture as a whole presented these parental characters well blended, although exhibiting a much wider range of variation than the F_1 generation of this cross. This variation appeared to indicate a relative segregation of the parental characters deserving of detail studies upon larger cultures. There were a number of plants similar to the parent hybrid, but none markedly nearer to *Lamarckiana*.

2. Progeny from hybrids 9ba, 9bb, and 9bc, *grandiflora* D × *biennis* B. These three hybrids (Davis, '10, p. 114) presented the parental characters well blended. They were essentially similar to *Lamarckiana* in flower structure and inflorescence, but differed in foliage and habit, the leaves on the lower portion of the stem being but half the length of those similarly placed on *Lamarckiana* and with only slight traces of crinkles; the habit was *biennis*-like.

From about 350 seedlings of hybrid 9ba, 76 plants were brought to maturity, being selected as representative types of the rosette stages. A small proportion of the rosettes was dwarfed and the nine selected representatives of this type developed small plants 1–2.5 dm. high, generally without side branches; these did not flower. The normal rosettes varied greatly in the forms of leaves and extent of the red coloration, certain ones being distinctly more like the respective parents of the cross than the average; these differences were maintained in the mature plants, but to a less marked degree. The culture in general presented a habit more *grandiflora*-like than *biennis*-like, but all of the characters remained blended, although there was a considerable range of variation in flower structure and foliage. While a number of the plants were similar to the hybrid parents, none proved to be appreciably nearer to *Lamarckiana*.

There were about 550 seedlings of hybrid 9bb, from which 93 plants, selected as representative rosettes, were brought to maturity. Relatively few dwarf rosettes were present in this culture; eleven of these being selected grew into plants 1–4 dm. high, small leaved and without prominent side branches, the larger of the dwarfs developing small *biennis*-like flowers. The culture in general was more uniform than the preceding, but certain rosettes and mature plants were noticeably more like one or the other of the original parents than the average, which presented these parental characters well blended. The foliage of the culture was distinctly crinkled so that the plants re-

sembled *Lamarckiana* more closely than those of the other cultures in the F_2 generation, differing chiefly in the smaller size of the basal leaves and in the absence of red tinted papillate glands on a green stem, the stem being mottled with red. One plant of this culture (10.12 Lz) was selected for marked peculiarities, but will not be described unless its behavior in an F_3 generation proves of sufficient interest.

About 800 seedlings of hybrid 9bc appeared in the culture, from which 95 plants were selected as representative types of rosettes. A few dwarf rosettes were present, six of which set in the ground developed into unbranched plants about 1 dm. high, that failed to flower. The culture in general exhibited considerable variation, the most interesting types of plants being several with light green, smooth, obtusely pointed leaves, similar in shape to *Lamarckiana,* but without crinkles. There was shown the same previously described tendency on the part of a few rosettes and mature plants to depart from the average of the culture towards the characteristics of the respective parents of the cross, maintaining, however, a blended structure of their parts.

Considering these cultures of F_2 generations in comparison with the F_1 generations that have been grown, the most striking feature is the greater range of variation exhibited not only by the F_2 plants as a whole, but by their different parts. Since the studies were not quantitative in character, because such a large proportion of the seedlings were necessarily discarded, it has not seemed best to describe the variations in detail and such an investigation is deferred for the present. However, in this increased variation is clearly indicated at least a relative segregation of the parental characters in the F_2 generation.[2]

[2] Extensive cultures from the seed of the two hybrids 10.30 La and 10.30 Lb, described in this paper, are now (February, 1911) seedlings with 4–5 leaves which already show marked segregation in this F_2 generation, with the extreme types closely resembling seedlings of the parents of the cross and between these a large range of intermediates.

The Possible Origin of *Œnothera Lamarckiana* as a Hybrid of *O. biennis* and *O. grandiflora*

We have shown that hybrids between certain strains of *Œnothera biennis* and *O. grandiflora* may be synthesized, which approach somewhat closely to *Œnothera Lamarckiana*, and there is good reason to believe that further experimentation will result in the production of forms with a more perfect resemblance. It is now important to ascertain, as far as this is possible, whether there are any historical reasons why *Lamarckiana* may not have arisen either accidentally or intentionally from such a cross.

Œnothera Lamarckiana appears to have been under cultivation in the gardens of the Muséum d'Histoire Naturelle at Paris in 1797, being described by Lamarck[3] under the name *grandiflora*. Shortly afterwards Seringe[4] renamed the form *Lamarckiana*, recognizing it to be distinct from the *grandiflora* of Aiton.

As previously noted from the investigations of MacDougal ('05) and Vail ('05), the evidence is very clear that *grandiflora* was introduced into England in 1778 and was at that time under cultivation at Kew. Forms of *Œnothera biennis* had of course been in European gardens for many years previous to 1778. There was therefore a period of about eighteen years (1778–1797) during which hybrids between *biennis* and *grandiflora* might have arisen in Europe before the earliest known record of the cultivation of *Œnothera Lamarckiana* in Paris. So striking an American novelty as *Œnothera grandiflora* would almost certainly have been passed on from Kew to other botanical gardens and in the interval between 1778 and 1797 is likely to have become widely distributed and cultivated. On historical grounds then there seems to be no reason with respect to the date of the first recorded recognition of *Œnothera Lamarckiana* why this form might not have arisen in Europe as a hybrid of *biennis* and *grandiflora*.

[3] "Encyclopédie Méthodique Botanique," Vol. IV, p. 554, 1797.

[4] De Candolle's "Prodomus," Vol. III, p. 47, 1828.

Let us suppose that it should be shown that *Œnothera Lamarckiana* was in existence previous to the date 1778, what effect would such evidence have on the hypothesis that the form is a hybrid of *biennis* and *grandiflora?* It would not in the writer's opinion have weight against experimental proof that *Lamarckiana* or forms closely resembling this plant may be synthesized as hybrids of these wild American species. It would not prove that Lamarck's plant in Paris (1797) was not a hybrid. It would merely indicate that *Lamarckiana,* having arisen as a hybrid in America, was introduced as such into Europe. As already pointed out, the position in *grandiflora* of the stigma well above the anthers gives ample opportunity for chance hybridization in nature. Indeed, the diverse forms that have appeared in my cultures from seed of *grandiflora* collected in the field clearly show that the species is far from homogeneous in character, a condition that is probably due to a large amount of cross pollination. It may be expected that careful search, especially in the southern United States, will bring to light occasional plants with characters intermediate between *grandiflora* and other species, such as, for example, southern types of *biennis,* but it is also probable that the behavior of such plants in culture will show them to be heterozygous in character, *i. e.,* hybrids.

There have been two attempts to establish the presence of *Lamarckiana* in Europe previous to 1778 when *grandiflora* was introduced at Kew. MacDougal ('07, pp. 5, 6) refers to *Lamarckiana* a description and figure of an *Œnothera* by Miller, Plate 189, Fig. 2, for the "Gardener's Dictionary," 1760. This figure, published in 1757, is of a large-flowered *Œnothera* with petals 2 or 2.2 cm. long and by its side (Fig. 1) is a smaller-flowered form. With respect to the point under discussion, the most important features of these figures, clearly shown by the drawing, is the position and form of the stigmas, *well below* the tips of the anthers and with the lobes *unexpanded* in open flowers. These are peculiarities of

biennis and, in the writer's experience, are not characteristic of *Lamarckiana* where the stigma lobes are usually expanded in the open flower and generally above or about on the level with the tips of the anthers. Furthermore the size of the petals in the illustration of the large-flowered type (Fig. 2) is no greater and indeed not so great as in some forms of *biennis*. Both of the figures show the essential characteristics of the flower of *biennis* to which they have generally been referred in taxonomic accounts. For these reasons the view of MacDougal that the illustration of the large-flowered type (Fig. 2) is of *Lamarckiana* and establishes its presence in Europe previous to 1757, is to the writer not convincing.

The second attempt to establish the presence of *Lamarckiana* in Europe previous to 1778 is the announcement of Gates ('10) that certain marginal notes in a copy of Bauhin's "Pinax," 1623, give in Latin an accurate description of this plant although differing in one or two minor characters. Gates presents an outline of the points which indicate to him that the description refers to *Lamarckiana*, but the notes themselves are not published. A full account is promised, in which we may expect to see these Latin notes and judge of them for ourselves, and comments on this announcement will be reserved for the present.

Finally we must return to the question of whether or not it appears probable that *Œnothera Lamarckiana* is at present a component of the American native flora. De Vries ('05, p. 368) refers to *Lamarckiana* certain herbarium material at the New York Botanical Garden and Missouri Botanical Garden, both collected by A. W. Chapman in Florida (1860 or earlier), and also material in the Philadelphia Academy of Science collected by C. W. Short at Lexington, Ky. A thorough search (MacDougal, '05, p. 6) by several botanists in the vicinity of Lexington Ky., Nashville Tenn., Knoxville Tenn., and Courtney Mo., in the endeavor to find living plants that might be identified as *Lamarckiana*, was unsuccess-

ful. Later, Miss Vail (MacDougal, '07, p. 67) came to the conclusion that the plant from Lexington, Ky., is *grandiflora,* and a possible escape from cultivation. I have not seen the herbarium material mentioned above, but in the light of the fact that many dried specimens could be prepared from my hybrids which as such would be considered *Lamarckiana,* it is clearly necessary that evidence from herbarium material should be weighed with much caution. The average herbarium material of the *Œnotheras* is generally not sufficient to show the peculiarities of the earlier phases of development (rosettes and basal foliage) which in the case of *Lamarckiana* furnish diagnostic characters that are necessary for a full identification. Unless the evidence of field collections is followed up by garden cultures, there is the possibility of numerous errors of interpretation.

A specimen in the Gray Herbarium of Harvard University is stated by MacDougal ('05, p. 5) to agree perfectly with *Œnothera Lamarckiana,* but in this view the writer can not accord. This plant was apparently grown in the Cambridge Botanical Garden, Massachusetts and bears the date 1862. The specimens are accompanied by the significant notes in the hand writing of Dr. Asa Gray "from seed of Thompson, Ipswich," and "said by English horticulturists to come from Texas." The flowers are large, with petals about 4.5 cm. long and sepals about 5 cm. long, very attenuate, the tips projecting 1 cm. beyond the folded petals in the manner characteristic of *grandiflora.* The stigma lobes are also *grandiflora*-like in their length, about 8 mm., and in their position, about 5 mm. above the tips of the anthers. A large detached leaf, about 18.5 cm. long, with some evidence of former crinkles, suggests by its form (although rather small) the basal leaves of *Lamarckiana.* The flowers and upper foliage of this specimen, however, agree very closely with broad-leaved types in my cultures of *grandiflora* and do not resemble the *Lamarckiana* that I have grown from seeds of De Vries, or with his figures and descriptions in "Die Mutations-

theorie.'' If this plant could be established as derived from *Œnotheras* introduced into England by Messrs. Carter and Co. at about 1860 from seeds said to come from Texas, it would be a point of great importance, as will appear in the following paragraphs.

De Vries ('05, pp. 384–385) offers strong evidence that the strains of *Lamarckiana* at present cultivated in Europe have a genetic relation to seed of Messrs. Carter and Co., of London about 1860. This seed is stated to have been received unnamed from Texas and plants grown from it were pronounced by Dr. Lindley to be *Lamarckiana*. A specimen from one of these plants is figured in "The Floral Magazine," Vol. II, Plate 78, 1862, this plate being reproduced in "L'Illustration Horticole," Vol. IX, Plate 318, 1862. This plate shows an *Œnothera* with flowers about 10 cm. (4 inches) in diameter and with a large amount of red coloration on the sepals and ovaries; the stigma is figured both above and below the tips of the anthers. The flowers of this illustration are larger than those of *Lamarckiana*, as known to the writer, and would do for *grandiflora* except for the position of the stigma which is much closer to the anthers than is typical for this species. The red coloration of the sepals and ovaries is much too deep for typical *Lamarckiana* and not unlike some forms of *grandiflora*, but the sepal tips, as drawn, are not so long or so pointed as in the latter form. Indeed the identification of this plate with any probable *Œnothera* is very difficult and the reasons why it should be called *Lamarckiana* are to the writer far from convincing, although it would perhaps be as easy to argue for this identification as for any other.

It is, however, possible that new light may be thrown on the composition of the cultures of Carter and Co. through the plant in the Gray Herbarium described above. The date of this specimen, 1862, together with the very suggestive notes of Dr. Gray "from seed of Thompson, Ipswich," and "said by English horticul-

turists to come from Texas,'' make it appear possible that this plant was derived from the cultures of Carter and Co. If this could be established it would indicate that forms very close to *grandiflora* were present in the cultures or seeds of this firm. It is not at all improbable that Texas with its immense area and very great range of climatic conditions may harbor *grandiflora* or related types especially since it is known to be rich in species of *Œnothera* and to have a number of large flowered representatives.

There may have been thus a second introduction into England of *grandiflora*-like types through Carter and Co. at about the year 1860. While there is of course no means of knowing whether their cultures were uniform, it is altogether probable that the results of their sowings gave a diverse progeny, since that has been my experience with seed from Alabama. There seems to be no reason why chance hybrids may not have been present or why *grandiflora*-like strains might not have shortly hybridized with European forms of *biennis*. These possibilities are mere matters of speculation to which little assistance is given by the puzzling plate in ''The Floral Magazine'' and in ''L'Illustration Horticole'' referred to above. A search among the English herbaria might, however, result in the discovery of specimens which would materially assist in the solution of a very interesting question—the identity of the plants grown by Carter and Co. At present the specimen in the Gray Herbarium appears to offer the most important evidence bearing upon the question. The contention that *Lamarckiana* was introduced in the form of a native American species at this date, 1860, seems to the writer to be without sufficient foundation.

The American botanist will ask himself why, if *Lamarckiana* was present in America as a native species in 1860, no localities are known where it may be observed in the field. It will be hard for him to believe that so strong and vigorous a plant, if a wild species, has become

so recently extinct when, as he well knows, the *Œnotheras* are established as remarkably successful forms in our flora. The fact that *Lamarckiana* is not known as a component of the native American flora stands as the most serious obstacle to the view that this plant is representative of a wild species. The writer believes it very probable that plants more or less resembling *Lamarckiana* will occasionally, or perhaps rarely, be found in parts of America and under circumstances indicating that they are not garden escapes, but it seems to him equally probable that these forms when tested in culture will give evidence of a heterozygous, or hybrid nature. The mere records of such plants as handed down by the average type of herbarium specimen, unaccompanied by experimental cultures, will have little or no value for the present problem—the origin of *Œnothera Lamarckiana*.

Summary

This paper offers a body of evidence which shows that hybrids resembling *Œnothera Lamarckiana* may be synthesized from certain strains of the American native species *O. biennis* and *O. grandiflora*. The resemblances of the hybrids to this plant are strongest with respect to the inflorescence, buds and flowers. The differences are chiefly manifest in the basal foliage of the mature plant, in the coloration of the stem, and in the more straggling habit of the hybrids. The rosettes of the hybrids present mixed forms of leaves, the younger with points of similarity to *Lamarckiana*. Bearing in mind that other strains of *biennis* have characteristics more *Lamarkiana*-like than those of strains A and B, herein described, it is more than probable that the hybrids from certain crosses made this season (1910), when grown in future cultures, will come closer to the desired end—the synthesis of a hybrid so similar to *Lamarckiana* as to be practically indistinguishable by the usual taxonomic tests.

Exception is taken to the claim of MacDougal ('07,

pp. 5, 6) that Miller's Plate 189, Fig. 2, for the "Gardener's Dictionary," 1760, establishes the presence of *Lamarckiana* in Europe previous to the date, 1778, when *grandiflora* is known to have been introduced into England. The view of De Vries that strains of *Lamarckiana* were introduced into England about 1860, through seed of Messrs. Carter and Co. said to come from Texas, is discussed with reference to certain specimens in the Gray Herbarium of Harvard University and in the light of the author's experience with seed from Alabama, indicating that Carter and Co. probably had *grandiflora*-like types in their cultures which were also likely to have been of a mixed character. The absence, so far as is known, of *Lamarckiana* as a component of the native American flora is emphasized as a point of great importance against the claim that *Lamarckiana* was introduced into Europe as an American wild species.

A working hypothesis is presented as a result of the writer's experimental studies and in relation to such historical evidence as is available, to the effect that *Œnothera Lamarckiana* arose as a hybrid between certain types of *biennis* and *grandiflora,* recognizing that under these names must, for the present at least, be included a number of races which can only be clearly defined by laborious genetical investigations. The precise time and place of such an origin for *Lamarckiana* is a matter of mere speculation, but there seems to the writer no good reason why hybridization between *biennis* and *grandiflora* might not have taken place in Europe between 1778 and 1797 (when *Lamarckiana* was first recognized at Paris) and also at later dates, as for example about 1860. It is also possible that *Lamarckiana* may have been introduced as a chance hybrid from America, but the probability of such an origin is naturally rather remote.

The bearing of the possible hybrid nature of *Œnothera Lamarckiana* upon the claim of De Vries that the behavior of this plant demonstrates the origin of new species

by mutation from a form representative of a typical wild species will be sufficiently evident to require no comment at this time. A discussion of the matter will therefore be reserved until the writer has proceeded further with his studies.

CAMBRIDGE, MASS.,
November, 1910.

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THE GENOTYPES OF MAIZE[1]

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THE doctrine of evolution had to overthrow the conception of permanency of specific types, generally held when Darwin's "Origin of Species" was published, because that conception was then associated with the idea of a separate original supernatural creation of each such type. It was Darwin's great triumph that he succeeded in marshaling such an array of facts pertaining to variability, as to convince the scientific world—and through the scientific world, ultimately the whole world—that everything is in a state of flux, and that there is no such thing as permanency among living things.

Owing to the work of De Vries and the other early students of modern genetics, permanency of type again demands serious scientific consideration, for such permanency is no longer incompatible with the doctrine of evolution, being now associated with some form of the mutation theory. The old idea of the immutability of specific types was based upon almost total ignorance of genetics, as was likewise the Darwinian conception of fluidity and gradual change, for although many appeals were made by Darwin to the experiences of plant and animal breeders, it is now known that these experiences were the result of no such careful control of conditions or analysis of results as has been found necessary for the discovery of genetic laws. The critical work of the past few years has wrought a great change and the new idea of permanency is gaining ground with the growth of experimental knowledge.

Without granting that we have yet reached a position in which we can say definitely that types are absolutely

[1] Read before the American Society of Naturalists, December, 1910.

permanent and do not, at least in some cases, gradually change into something new, the large accumulation of

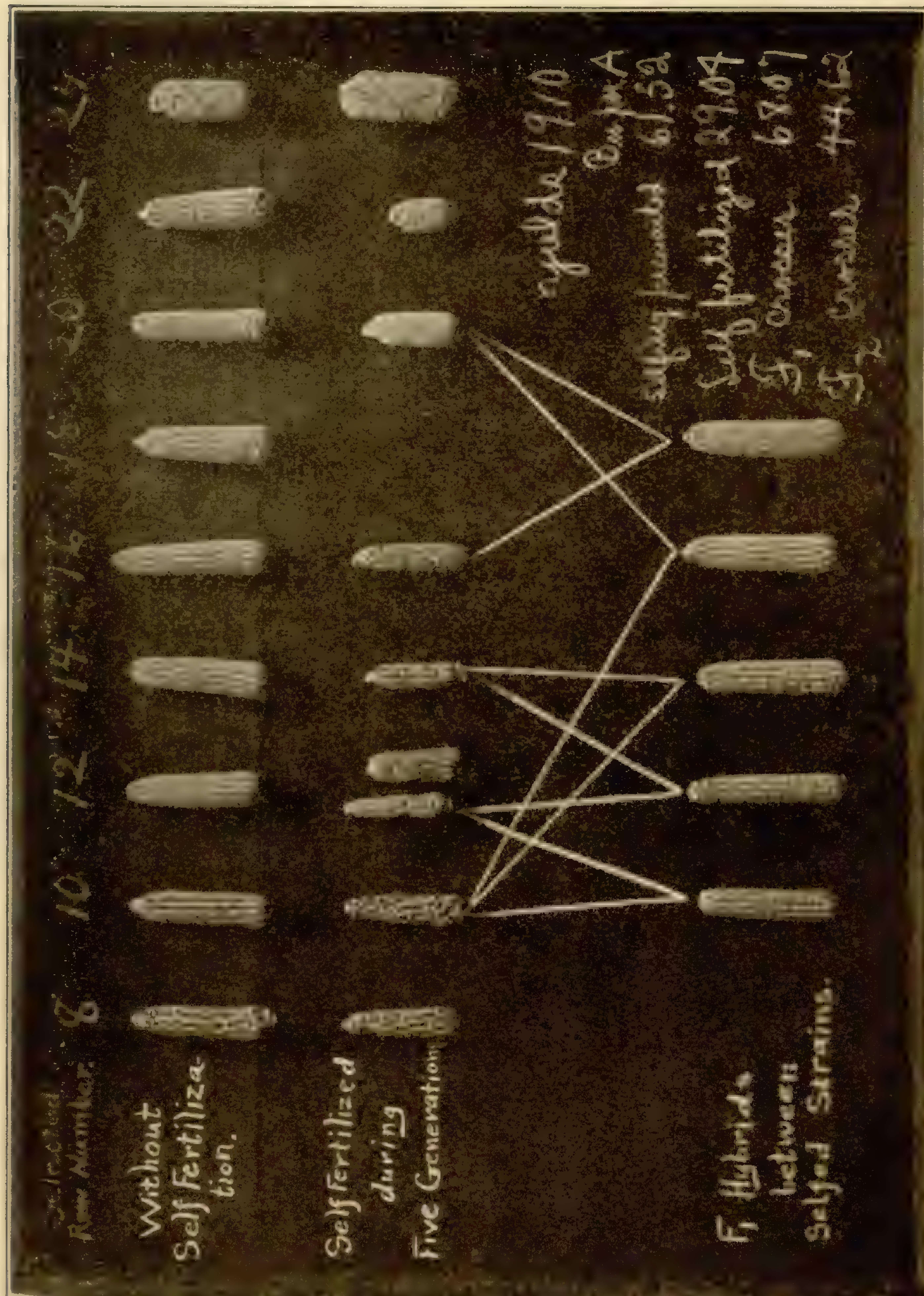

FIG. 1. Each ear in this exhibit represents a different pedigreed family. In each family the variation was slight, and the ear chosen for the exhibit was fairly representative of the entire family. The two self-fertilized ears under selection number "12" belong to two distinct strains, the left-hand one being my "Strain A" of other publications. During the last two years this has been selected to its own modal number, while the right-hand ear has been selected to twelve rows throughout the course of the experiments.

experimental data now available makes it necessary to recognize a clear distinction between the evolutionary changes in types, on the one hand, and the fluctuations within each type, on the other hand.

Quite naturally the first experimental evidence of the existence of permanent hereditary types involved only such characteristics as are clearly distinguishable upon inspection. Thus Jordan was able to demonstrate that within the systematic species *Draba verna* there are included as many as two-hundred hereditary forms, whose distinguishing characteristics appear unchanged from generation to generation, in such manner that his pedigrees of these forms were clearly and permanently distinguishable from each other by easily defined morphological features. Such "*petites espèces*" or "little species" (afterwards called by De Vries "elementary species," and by Johannsen "biotypes" or "genotypes"), have since been observed by Wittrock and his students, and by many others, in a great number of wild species, and they are now quite generally supposed to be of almost universal occurrence.

About 1890 N. H. Nilsson made a similar discovery in connection with his breeding of wheat, oats, barley and other grains at Svalöf, Sweden, but his work remained practically unknown to the scientific world until it was brought to light several years ago by De Vries. Nilsson found in these grains elementary species, each with its own morphological characters and its own specific capacity to yield crops of given size or quality under given external conditions. More recently, sharp-eyed taxonomists have been rapidly raising many of the elementary species of wild plants to the rank of systematic species.

It was natural that the earliest genotypes recognized, such as those of Jordan and Nilsson, should have possessed visibly discrete characteristics, and that they should first have become familiar in normally self-fertilized plants, among which little confusion is occasioned

by the rare crossing of unlike individuals. Great credit is due to Johannsen[2] for demonstrating that in such self-fertilized plants, types also exist which are not readily distinguishable by simple inspection, but whose occurrence may be completely demonstrated by the refined methods of the mathematician. Not only has Johannsen's work been so extensive as to justify the conclusions arrived at by him, but various other investigators, working with different classes of research material, have shown that the conditions found by Johannsen in beans and barley are duplicated in many other species and varieties. Perhaps the strongest support in this direction has come from the work of East[3] with potatoes and that of Jennings[4] with various microscopic organisms, especially with paramecium.

The fact that *Draba verna*, and many other wild species in which the existence of numerous elementary species has been demonstrated, as well as wheat, oats, barley and beans, are all predominantly self-fertilizing, and that potatoes and paramecium have an asexual reproduction, has led some to the erroneous notion that the discreteness, uniformity and permanence of the types which have been discovered among these and other similar organisms, are in some way dependent upon the absence of crossing.

It must be admitted that conclusions drawn from self-fertilized and asexual material do not necessarily apply to plants and animals whose successful existence is dependent upon repeated crossing. Nevertheless, the conception of pure and permanent genotypes in cross-bred material has become familiar simultaneously, owing to the work done in Mendelian heredity; for homozygous

[2] Johannsen, W., "Ueber Erblichkeit in Populationen und in reinen Linien," 68 pp., Jena, 1903.

[3] East, E. M., "The transmission of variations in the potato in asexual reproduction," Conn. Exp. Sta. Report 1909–1910, pp. 119–160, 5 pls.

[4] Jennings, H. S., "Heredity, variation and evolution in Protozoa—II. Heredity and variation of size and form in Paramecium, with studies of growth, environmental action and selection," *Proc. Amer. Phil. Soc.*, 47: 393–546, 1908.

combinations of the various characteristics of plants and animals "breed true" to those characteristics. Just as the first recognition of permanent differences in pure lines involved easily distinguishable characters, so also these first discoveries of permanent pure-breeding genotypes in cross-bred plants and animals involved easily definable morphological characteristics. The demonstration that in normally pure-bred lines there are distinctions more minute than such easily visible features as characterize the elementary forms of Draba and many other species, was an important advance in our analysis of the populations which make up the species of plants and animals. A similar demonstration that populations of cross-breeding plants and animals are composed of fundamentally distinct types, intermingled but not changed by panmixia, and capable of being separated by appropriate means and of being shown to possess the discreteness, uniformity and permanence already demonstrated for the genotypes of self-fertilized and clonal races, will add greatly to the importance of the fundamental conception of permanency of types involved in the work of De Vries and Johannsen.

For the study of this problem there is probably no better plant than Indian corn. It is known to exist in a large number of obviously distinct strains or subspecies which cross together with the greatest ease. Many of its characteristics have been proved by different investigators to be Mendelian unit-characters; such, for instance, as the color of the seed-coat, whether red, dark yellow, light yellow, variegated or colorless, the color of the aleurone layer, whether blue, red or white; the color of the endosperm, whether yellow or white; the chemical composition of the endosperm, whether starchy or sugary, the color of the silks and cobs whether red or white, etc. It has become known also, mainly through the excellent work done at the Illinois State Experiment Station, that oil-content and protein-content of the grains, the position of the ears, the number of ears on the stalk, and

several other characters, are capable of accentuation by selection, so that different degrees of these qualities are capable of being made characteristics of particular strains of corn, without there being the least evidence as yet that these last-mentioned qualities bear any relation to the unit-characters with which the student of genetics generally deals. A further point in favor of maize as a subject for the study of genotypes among cross-breeding organisms lies in the fact that its flowers are so arranged that, while self-fertilization is possible, it is naturally almost completely excluded, thus ensuring the same relations as are presented by bi-sexual or diœcious plants and animals, while retaining the means of conveniently testing the genotypic nature of each individual by controlled self-fertilizations.

I think I have demonstrated during the last five years that there are many genotypes of Indian corn which, although they can not always be distinguished by definable external characteristics, can be proved to be just as certainly and permanently discrete as the types whose distinguishing features can be recognized as Mendelian unit-characters. I shall endeavor to show, in what follows, a portion of the evidence which leads me to this conclusion.

In 1905 I undertook a rather extensive series of comparisons between cross-bred and self-fertilized strains of Indian corn for the purpose of discovering the effects of these methods of breeding upon variability, and these investigations have been continued each year since that time. Two phenomena immediately attracted my attention: First, the well-known fact that the children of self-fertilized parents are inferior to those of cross-fertilized parents in height, yield and other characters dependent in any way upon physiological vigor. In every instance this phenomenon was plainly evident in the very first generation after self-fertilization. This decrease in physiological vigor due to self-fertilization has become an

extremely important relation in the study of the genotypes, as will be shown later.

The second phenomenon which quickly made itself manifest, was first clearly appreciated in the second generation after the beginning of the experiments; this was the fact that each self-fertilized family possessed morphological features which clearly differentiated it from all other families. In most cases the distinguishing characteristics of these families were of such elusive nature that it was impossible to recognize definite unit-characters, and indeed, morphological descriptions of the several pedigrees could often be made only in terms of greater or less intensity of the several qualities exhibited. However, the distinctions were real and applied to every member of the particular family. Thus one family might have a very slender, poorly developed male panicle, while another would have more thick and dense branches of the panicle. This difference might be quite small when given in actual measurement but inspection showed that every individual of the one family had the slender, illy developed panicles, while all of the offspring of the other family had the thicker, denser type. Similarly, one family might have a slightly broader and darker green leaf than another, and these characteristic differences were likewise uniformly present in all members of the single families contrasted. No such character as this is capable of being traced through the generations following a cross, in the manner usually pursued by the geneticist, and the matter must be approached by indirect methods. The important point to be kept in mind here is simply that *the self-fertilized families, derived originally from a common stock, do differ by morphological characteristics*, and that there comes to be great uniformity in regard to the presence of these characteristics in all the individuals of a given self-fertilized family.

This relative uniformity, which is so obvious even to the casual observer, is not sufficient in itself, however,

to positively demonstrate the existence of distinct genotypes in maize, because the slight variations which must always be present even in the most uniform progeny, can not be certainly distinguished as genotypic or fluctuating simply by inspection. Such demonstration must rest upon a combination of biometric and genetic evidence in order to prove acceptable. Most of the differentiating characters of my several strains of maize are such that they do not lend themselves readily to biometric methods, but the number of rows on the ear is well adapted for such study and several important results have been derived from the consideration of this character. An important proof that the self-fertilized families derived from my common original stock of corn are genotypically distinct, and that they do not owe their different morphological and physiological qualities to fluctuations within a single genotype, was quickly found in the fact that two of these families selected respectively to 12 and 14 rows of grains on the ears, showed a regression of row-number toward different centers instead of toward a common center. The mean of the original population was slightly above 14 rows. The selection to 14 rows was very near this mean and the selection to 12 rows considerably below it. According to Galton's well-known law of "regression toward mediocrity," the mean of a family whose parents were selected to 12 rows should have lain somewhat above 12 rows, and that selected to 14 rows should have retained the mean approximately at 14 rows. The actual result in the case of selection to 12 rows was the production of a family having a mean row-number considerably below the number of rows selected, and the subsequent generations have since shown a close approach to an 8-rowed condition; while the family whose parents were in each generation selected to 14 rows has always had the mean very near to 14 rows. As these families were grown under as nearly uniform conditions as possible, the fact that the 14-rowed family continues

to have its mean row-number at 14 shows that the fall in row-number from 12 to 8 in the other family has been due to internal rather than to external causes.

The change in variability in number of rows on the ears has also been studied from year to year. Continued self-fertilization has resulted in a gradual decrease of variability in the number of rows per ear in each of the self-fertilized lines. This is a fluctuating character, and so far as present evidence goes, the number of rows per ear in any strain can not be fixed at a definite number. While it is probable that none of my self-fertilized families has yet reached an absolutely pure-bred condition, several of them have become so nearly pure-bred that their various relations can be used to demonstrate that they are approaching purity as a limit.

In 1909 two of these nearly pure-bred families were compared with their reciprocal hybrids in the first and second generations, with reference to the variability in number of rows.[5] It was found that the average variability in these two self-fertilized families was 9.08 per cent. The variation in number of rows in their F_1 progeny was 9.06 per cent., and in the F_2 12.63 per cent. A comparison of these coefficients of variability shows at once that the variation in number of rows in the F_1 is essentially identical with that in the self-fertilized lines used for the cross. Theoretically this should be so if the strains used were pure genotypes, because in that case all germ-cells in each pure strain were alike, and therefore, when individuals belonging to these two lines were crossed, equal sperms met equal eggs; consequently there should be no variability in their offspring due to germinal differences, but only those due to environment in the widest sense. As the pure-bred families and their F_1 and F_2 progenies were grown beside each other during the same season, they were subjected to as nearly identical environmental influences as can be attained.

[5] Shull, G. H., "Hybridization methods in corn breeding," *Am. Breeders' Magazine*, 1: 98–107, 1910.

Consequently, when the F_1 shows the same variability as the pure lines which entered into it we must conclude that there was at least approximate equality among the sperms which came from the one self-fertilized strain, and among the eggs which came from the other. In the F_2, on the other hand, genotypic differences appear, owing to the segregation of the different characteristics into the different germ-cells, and to this fact may be ascribed the increased variability in the F_2.

While other characters have not been studied by the same methods that have been used in the investigation of the number of rows on the ears, several features associated with the physiological vigor of the various pedigrees have given evidence which appears to me to be strongly corroboratory of the uniformity of the germ-cells produced by plants which have become pure-bred through continued self-fertilization. The smaller size and less vigor of the offspring of self-fertilized plants as compared with those from a normally cross-bred plant were formerly taken to indicate that self-fertilization is injurious, and Darwin's "Effects of Cross and Self-fertilization in the Vegetable Kingdom" strongly impressed this point of view. I have been able to demonstrate, however, that this supposedly injurious effect of self-fertilization is only apparent and not real; or at least that if there is such injurious effect, it is relatively insignificant as compared with the increased vigor due to heterozygosis. The most important evidence of this is found in the fact that the continuation of self-fertilization in any pedigree does not produce a corresponding decrease in vitality and size. The decrease resulting from a second year of self-fertilization is not as great as that from the first year. The third year of self-fertilization produces still less deterioration, and as this process is continued a limit is approached in such manner as to justify the inference that when complete purity is attained no further deterioration is to be expected, thus proving that self-fertilization is not in itself injurious.

That this is also true of other plants is derivable from Darwin's own work.

This decrease in size and vigor is accompanied by the gradual lessening of variability, and when that state is finally reached in which there is no further decrease in size and vigor, it seems probable that there will be also no further noticeable change in variability. This does not mean, of course, that there will be no variability, for even the most uniform group of plants or animals will of necessity show slight variations produced by different conditions of life, food supply and so forth. But present evidence does not warrant the belief that such fluctuations affect in the least the fundamental qualities of the genotype.

In 1908 I suggested a hypothesis to explain the apparent deterioration attendant upon self-fertilization, by pointing out that in plants, such as maize, which show superiority as a result of cross-fertilization, this superiority is of the same nature as that so generally met with in F_1 hybrids. I assumed that the vigor in such cases is due to the presence of heterozygous elements in the hybrids, and that the degree of vigor is correlated with the number of characters in respect to which the hybrids are heterozygous. I do not believe that this correlation is perfect, of course, but approximate, as it is readily conceivable that even though the general principle should be correct, heterozygosis in some elements may be without effect upon vigor, or even depressing. The presence of unpaired genes, or the presence of unlike or unequal paired genes, was assumed to produce the greater functional activity upon which larger size and greater efficiency depend. This idea has been elaborated by Dr. East[6] and shown to agree with his own extensive experiments in self-fertilizing and crossing maize. He suggests that this stimulation due to hybridity may be analogous to that of ionization.

Mr. A. B. Bruce proposes a slightly different hypothe-

[6] East, E. M., "The distinction between development and heredity in in-breeding," AMER. NAT., 43: 173–181, 1909.

sis in which the degree of vigor is assumed to depend upon the number of *dominant* elements present rather than the number of *heterozygous* elements. While all of my data thus far are in perfect accord with my own hypothesis, and I know of no instance in which self-fertilization of a corn-plant of maximum vigor has not resulted in a less vigorous progeny, it is quite possible that I have still insufficient data from which to distinguish between the results expected under these two hypotheses. However, for the purpose of the present discussion, it is not necessary to decide which of these two hypotheses (if either) is correct. Both of them are based upon the view that the germ-cells produced by any plant whose vigor has been increased by crossing are not uniform, some possessing positive elements or genes not possessed by others.

Several different characters which are more or less dependent upon physiological vigor have been taken into account in my work, each of which gives its own support to the conception upon which both of these hypotheses are based. The number of rows of grains on the ears which has been most extensively used as a measure of variability, and as a guide in selection, is found to be somewhat affected by the vigor of the individual, and it is due to this fact, no doubt, that the row-number is a fluctuating character, even in the pure genotype. Another characteristic which has been used as a measure of vigor has been the yield of corn computed in bushels per acre.[7] A third characteristic, which was not taken into account at the beginning of the experiments but which has given confirmatory data in the later years, is the height of the stalks, a character which was much used by Darwin as a measure of vigor in his study of the effects of cross- and self-fertilization in plants.

[7] It should be understood that this method of stating yields is seriously defective, in that it implies the existence of a much smaller probable error than is actually present, since each of my pedigrees has usually occupied only about one one-hundredth of an acre. However, I believe that this defect is more than offset by the advantage of using a unit of yield with which all readers are familiar.

We may now consider the behavior of these several measures of physiological vigor in relation to the theory that distinct genotypes of maize are gradually segregated from their hybrid combinations, by self-fertilization, and that the degree of vigor is correlated with the degree of heterozygosis.

I have kept families selected to given numbers of rows on the ears—one series of families repeatedly self-fertilized and another series repeatedly crossed with mixed pollen in such a manner that self-fertilization is precluded by artificial means. It is not practicable to do this crossing with mixed pollen in such a manner as to duplicate the conditions found in an ordinary corn-field for the simple reason that the number of individuals which contribute the pollen must be more greatly restricted than is true in the open field. While self-fertilization has been entirely prevented, there has been a degree of in-breeding somewhat greater therefore than will occur under non-experimental conditions. This degree of in-breeding is sufficient to slowly eliminate some of the hybrid elements which were originally in my strain of corn and should consequently lead to a gradual deterioration in case my theory of the relation between vigor and hybridity is correct. As a matter of fact, such deterioration has become apparent in the "cross-bred"[8] families, when measured either by height of stalk or yield per acre, though both of these measures show that the deterioration has been slight. It is so slight, indeed, that it is very much exceeded by the fluctuations from season to season, and may only be demonstrated by the application of a correction which approximately eliminates this seasonal fluctuation. When we compare this continual slight fall in physiological vigor of the cross-

[8] It should be noted that here and in what follows I use the expression "cross-bred" in a special sense, to denote the fact that all self-fertilization has been avoided. The more usual use of the term "cross-bred" to denote a cross between individuals belonging to distinct strains, I replace in this paper by the expression "F_1," as I can see no tangible distinction between such a cross, and hybridization in the older, more restricted, and more arbitrary sense.

bred families with the changes produced in the self-fertilized families during the same period, there is a striking contrast, for in the latter case there was great decrease in height and yield in the first year, a considerably less decrease in the second year of self-fertilization, still less in the third year, and so on, and while I have evidence that none of my self-fertilized families has yet reached a state of perfect stability, they are at the present time decreasing in regard to both of these measures of vigor somewhat less rapidly under continued self-fertilization than are the families in which self-fertilization has been absolutely precluded.

Necessary corollaries of the view that the degree of vigor is dependent on the degree of hybridity, or, in other words, that it is dependent roughly upon the number of heterozygous elements present and not upon any injurious effect of in-breeding *per se*, are (*a*) that when two plants in the same self-fertilized family, or within the same genotype, however distantly the chosen individuals may be related, are bred together, there shall be no increase of vigor over that shown by self-fertilized plants in the same genotype, since no new hereditary element is introduced by such a cross; (*b*) that first generation hybrids produced by crossing individuals belonging to two self-fertilized lines, or pure genotypes, will show the highest degree of vigor possible in progenies representing combinations of those two genotypes, because in the first generation every individual will be heterozygous with respect to all of the characters which differentiate the two genotypes to which the chosen parents belong, while in subsequent generations, recombination of these characters will decrease the average number of heterozygous genes present in each individual; (*c*) that crosses between sibs among the first-generation hybrids between two genotypes will yield progenies having the same characteristics, the same vigor, and the same degree of heterogeneity, as will be shown by the progenies of self-fertilized plants belonging to the same first-generation family.

All of these propositions have now been tested in a limited way. In 1910 nine different self-fertilized families were compared with nine crosses between sibs within the same self-fertilized family; ten crosses between sibs in F_1 families were compared with ten self-fertilizations in the same F_1 families; seven families were raised as first generation hybrids between individuals belonging to different self-fertilized families; and ten families were grown, in which self-fertilization had been entirely precluded during the past five years. The average height of plants in decimeters, the average number of rows per ear, and the average yield in bushels per acre, in these fifty-five families are given in the following table:

	Selfed × Self	Selfed × Sibs	F_1	F_2	F_1 × Self	F_1 × Sibs	Cross-breds
Av. Height	19.28	20.00	25.00	23.42	23.55	23.30	22.95
Av. Rows	12.28	13.26	14.41	13.67	13.615	13.73	15.13
Av. Yield	29.04	30.17	68.07	44.62	41.77	47.465	61.52

An examination of this table indicates to me that on the whole my self-fertilized families are not yet quite pure-bred; for the sib crosses give on the average a slightly greater height, number of rows per ear, and yield per acre than the corresponding self-fertilized families, as shown by a comparison of the first two columns of the table. The same fact is apparent from a comparison of the "F_1 × self" and "F_1 × Sibs" columns, except that in this case the heights and number of rows per ear are essentially equal while the yield per acre is significantly higher in the sib-crosses than in the self-fertilized families. An alternative explanation of these slight differences between the results of self-fertilization and of sib-crosses may attribute them to an injurious effect of self-fertilization, but in any event such injurious effect must be exceedingly slight as compared with the stimulating effect of heterozygosis. My practise of choosing for seed the best available ears tends to delay the attainment of complete genotypic purity, and this fact favors the view that whatever advantages the sib-

crosses show, are attributable to this lack of purity, rather than to any advantage gained by crossing *per se*.

The columns of the table representing the F_1 and F_2 show very plainly the superiority of the former over the latter in regard to both height and yield per acre. The fall in average height from F_1 to F_2 from 25 decimeters to 23.4 decimeters and the corresponding fall in yield per acre from 68.07 bushels in the F_1 to 44.62 bushels per acre in the F_2 show in a most striking way the economic advantage of using first-generation hybrids for producing the corn crop. A comparison of the F_1 hybrids with the "cross-breds" shows the average yield of the former to be 6.55 bushels per acre greater than that in the families in which self-fertilization had been avoided.

The relation of these results to the experiences of economic breeders of corn may now be considered. Perhaps in no other class of plants has the evidence been so strong for the possibility of gradual improvement through continued selection as in corn, and this method has been generally followed. The selections of particular physical and chemical qualities which have been carried on at various experiment stations have produced noteworthy results. Most important instances of this kind are involved in the breeding experiences of Hopkins, Smith and other breeders at the Illinois State Experiment Station, which have been already mentioned. Here selections for high oil content, low oil content, high protein and low protein, high ears and low ears, and the angle which the ears make with the axis of the plant, as well as selection for increased yields, have all led to the production of strains which possessed the desired qualities to a much higher degree than that in which they existed in the foundation stock when the selection began. All of these results may be readily explained on the ground that some hybrid combinations of genotypes have greater capacity for the production of the desired qualities than other combinations, and that the selection has gradually brought about the segregation of those genotype-combinations

which had the highest capacity for the production of the desired qualities. At least in regard to yield and not improbably also in regard to the other qualities for which selections were made, the results were dependent, not upon the isolation of pure types possessing the desired quality, but upon the securing and maintaining the proper combination of types. I have shown above that segregation takes place in a manner at least similar to, if not identical with, the well-known behavior of Mendelian characters. As a consequence of this, no strain of corn can be maintained at a high value with respect to any quality whose development is correlated with heterozygosis, except by continued selection for the particular qualities desired. If in any such specialized strain selections should be made for a few years on the basis of some character independent of the one used in establishing the strain, the superior qualities for which it was originally selected would quickly disappear, owing to the breaking up of the efficient combinations which had been segregated and maintained by selection.

The principles here presented have very great potential consequence for the practical grower of corn, and possibly for the breeder of many other cross-breeding plants and of animals. Their importance seems not to have been fully appreciated by any one however, until recently, though several breeders appear to have glimpsed the possibilities at one time or another. Thus G. N. Collins,[9] of the United States Department of Agriculture, has recently shown that several breeders at different times began experiments to test the value of hybridization in the production of high-yielding strains of corn. The first attempt of this kind which he has found was that of W. J. Beal[10] at the Michigan Agricultural College in 1876. At Professor Beal's instance several other experiment stations undertook to work in co-operation with the Michigan Station in testing the value of hybrids in

[9] Collins, G. N., "The value of first generation hybrids in corn," Bull. 191, U. S. Bureau of Plant Industry, 45 pp., 1910.

[10] Beal; W. J., Reports, Michigan Board of Agriculture, 1876–1881.

corn breeding, but only Professor Ingersoll,[11] of Purdue University, reported results. Professor Sanborn[12] apparently performed similar experiments in the late eighties at the Maine Agricultural Experiment Station. In 1892 G. W. McCluer[13] reported on a number of crosses made during the preceding two years at the Illinois Agricultural Experiment Station, and during the next two years Morrow and Gardner[14] published bulletins from the same station, describing the results of a number of crosses. Apparently none of this work led to the subsequent utilization of hybridization methods in corn breeding, as no work along this line appears to have been done between the time when Morrow and Gardner issued their second bulletin in 1893 and the publication of the first report of my work with corn at the Station for Experimental Evolution in 1908. The work of Beal, Ingersoll, Sanborn, McCluer, and Morrow and Gardner showed that increased yields from the hybrids, as compared with the strains used for the crosses, are the almost invariable result, though both McCluer, and Morrow and Gardner found isolated instances in which the hybrids were inferior to the parent strains. Hartley[15] has since reported that among a number of crosses made by the United States Department of Agriculture also, some gave poorer yields than the parent strains used for the cross, while others gave superior yields, and reached the conclusion, which I think is justified by my own results, that promiscuous crossing is not necessarily advantageous but that certain combinations lead to increased yields while others may prove disadvantageous. Collins[16] has

[11] Seventh Annual Report of Purdue University, 1881, p. 87.

[12] Sanborn, J. W., "Indian corn." Agriculture of Maine, 33d Annual Report, Maine Board of Agriculture, 1889–90, p. 78.

[13] McCluer, G. W., "Corn crossing." Bull. 21, Illinois Agr. Exp. Sta., 1892, p. 85.

[14] Morrow, G. E., and Gardner, F. D., Bulletin 25, pp. 179–180, and Bulletin 31, pp. 359–360, Illinois Agr. Exp. Sta., 1893 and 1894.

[15] Hartley, C. P., "Progress in methods of producing higher yielding strains of corn," Yearbook, U. S. Dept. Agr., 1909, pp. 309–320, 4 pls.

[16] *Op. cit.*

also reported on sixteen hybrid combinations all but two of which gave increased yields in the F_1. From the work of all these men, especially from my own comparisons between F_1 and F_2 hybrids, it has become obvious that the secret of the highest success in corn breeding from an economic point of view lies in finding those strains which will produce the largest yield and then utilizing the first-generation hybrids each year.

The point which most interests us on the present occasion is not, however, the economic importance of using first generation crosses, but the evidence which appears to me clearly indicate that a normally cross-bred plant like Indian corn harmonizes in its fundamental nature with such normally self-fertilized material as beans, wheat and other grains, and such clonal varieties as potatoes, paramecium, etc., that the egg-cells and sperm-cells of even the most complex hybrids present a limited number of different types which can be assorted into homozygous combinations, and that, therefore, the progressive change resulting from continued selection may be simply explained as the gradual segregation of homozygous types or of the most efficient heterozygous combinations.

The fact that yield and perhaps many other qualities attain their highest development in the case of complex hybrids naturally leads to the unconscious selection of heterozygous plants for the next year's cultures, and the continual breaking up of these complex hybrids in subsequent generations gives a result which closely resembles fluctuating variation, but which is fundamentally different from it. The genuineness of the gains made by selection in corn might naturally lead to the conclusion that fluctuations are inherited were it not for the abundant evidence now available showing that a considerable portion of the variation presented is not fluctuational, but is due to the presence of a mixture of different types which any selection partially segregates.

NOTES AND LITERATURE

IS THE FEMALE FROG HETEROZYGOUS IN REGARD TO SEX-DETERMINATION?

The evidence that sex is determined by an internal mechanism in unisexual animals has accumulated rapidly in the last few years. The one outstanding case is that of the frog. That extreme variations in the sex ratio occur in this amphibian has been evident from the early experiments of Born 1881, Pflüger 1882, and Yung 1883–85. The effects were generally ascribed by the earlier workers to differences in the food of the tadpole. Most recent and more carefully controlled experiments, notably those of Cuénot and of King, have shown beyond doubt that food is not a factor that determines the sex of the tadpole. On the other hand, Richard Hertwig has effected astonishing changes in the sex ratio of the frog by delaying fertilization of the eggs. Over-ripe eggs produce a high percentage of males. This conclusion has been recently confirmed and extended by a student of Hertwig's, Sergius Kuschakewitsch.[1] By delaying fertilization of the eggs for 89 hours after the first eggs had been laid (which gave 53 per cent. of males) there was produced 100 per cent. of males. The death rate of the larvæ was so low (from 4 to 6 per cent.) that it could not have seriously affected the results. The following table gives the outcome of Hertwig's observations and those of Kuschakewitsch.

Author	Hours 0	Hours 6	Hours 18	Hours 24	Hours 36	Hours 42	Hours 54	Hours 64	Hours 89
R. Hertwig, 1907	58%	54%	—	55%	—	—	87%	—	—
"	49	—	—	—	58%	—	59	—	—
"	48.5	—	37%	—	—	50%	—	88%	—
Kuschakewitsch	53	—	—	—	—	—	—	—	100%

This evidence shows beyond question that the *sex ratio* is affected by delay in fertilization, and may seem to show even that *sex itself* is determined by this factor. The evidence will, however, bear closer scrutiny. The frogs, *Rana esculenta,* were captured while pairing, and were allowed to lay a few eggs in

[1] Hertwig's Festschrift, 1910.

confinement, when they were separated. After 89 hours the female was killed, the remainder of her eggs placed on glass slides, and fertilized with a decoction of the testes of other (one or more?) males. If many of the eggs soon rotated within their membranes this was taken as a sign of successful fertilization. It will be noted that a different male from that employed for the normal fertilization was necessarily employed, because the original male had presumably lost his power to further fertilize. The employment of different males introduces a possible error into the results, for, if the male is heterozygous for sex determination, it is conceivable, as I have previously pointed out in reviewing Hertwig's results, that in different individuals the sperm may be differently affected in regard to its fertilization power. At present we have no evidence to show that in male frogs such differences exist, and it seems unlikely that such consistent results as these of Hertwig and of Kuschakewitsch can be explained in this way. An alternative view is, however, possible. If the female is heterozygous for sex production, and in consequence two kinds of eggs are produced, it may be that the female determining eggs are more injured by delay than are those of the other class, the male-determining eggs. It becomes, therefore, imperative to know what proportion of eggs were fertilized in these experiments, Unfortunately this critical evidence is omitted from Kuschakewitsch's paper. He states that the death rate of the tadpoles that emerge is low, but one looks in vain for information relating to the number of eggs that were fertilized. Therefore until this datum is forthcoming it is not possible to draw any certain conclusions in regard to sex determination from the evidence published by the author.

T. H. MORGAN.

COLUMBIA UNIVERSITY.

THE MUTATION THEORY

The publication of the first volume of DeVries's "Mutationstheorie" in 1901, together with the rediscovery of Mendel's principles, served to bring about a period of unprecedented activity in the study of the problems connected with variation, heredity and evolution. While the results of this decade of work have probably raised as many questions as they have answered, yet the period has undoubtedly been marked by advances of the first importance, both in methods of investigation and in

results and the point of view achieved. This stimulus we owe in no small measure to the author of "Die Mutationstheorie." During this period DeVries himself has continued his activities uninterrupted except by his two visits to America, in which he did much through his letters and the publication of his "Species and Varieties" and "Plant Breeding," to familiarize his views to American biologists. However, the actual detailed data upon which his theory was based, remained largely a sealed book except to readers of German. Even those engaged in active work on these subjects frequently failed to acquaint themselves sufficiently with "Die Mutationstheorie" before breaking into the field of controversy. Particularly is this true of the second volume, the contents of which have been in large part neglected.

Professor Farmer and Mr. Darbishire have therefore performed an important service in translating this work into English. The first volume of their translation[1] is the subject of this review. The second volume is promised for April. The work will undoubtedly receive a wide reading by English-speaking biologists, and by others as well. The translation is an excellent one, faithful to the German meaning but rendered into idiomatic English. Whatever the degree of one's familiarity with the German edition, a perusal of the work in English will be found profitable and stimulating.

A few remarks regarding the contents of the book itself may not be out of place. In a re-perusal of the work, one is struck with the optimism of its author and with the brilliancy and breadth of his exposition of the views set forth. It is not necessary to agree with these views in their entirety in order to appreciate these qualities of the book. The analysis of the data amassed by Darwin, in which it is shown that Darwin's *single variations* are the same as De Vries's mutations, seems to the reviewer particularly effective. The conception of elementary species seems also one which will be of lasting value, having already shed a flood of light on many problems.

Probably the time will soon come when nearly all biologists will be ready to admit that mutation, or the sudden appearance of new forms, has been an important factor at least, in species formation in plants and animals. Admitting this, it remains to be discovered what relation these sudden appearances bear to the gen-

[1] DeVries, Hugo, 1909, "The Mutation Theory." Translated by Professor J. B. Farmer and A. D. Darbishire. Volume I. Six colored plates, figs. 119, pp. 582. Chicago, The Open Court Publishing Co.

eral trends of evolution, which are apparent in so many phylogenies. This larger problem, which may not be amenable to direct experimental attack, will probably occupy evolutionists for many years to come. For, granting the facts of mutation, we have only accounted for a micro-evolution, and it has still to be shown that the larger tendencies can be sufficiently accounted for by the same means, without the intervention of other factors.

While the supreme importance of DeVries's investigations on mutation in *Œnothera* is fully recognized, his premutation theory has always seemed to the reviewer unsatisfactory as a hypothesis to explain the material basis of these phenomena. The cytological investigations of myself and others on these forms have determined the events of germ cell formation, some of which provide a possible basis for the sudden appearance of new types. They have, moreover, shown that different cytological processes are involved in the origin of different mutants, and in this way have thrown much light on the relationships of some of the mutants to their parent form. It is probable that the whole question of the relation of the mutants to their parent will be found to be much more complex than at present supposed.

R. R. GATES.

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THE INHERITANCE OF POLYMORPHISM AND SEX IN COLIAS PHILODICE[1]

PROFESSOR JOHN H. GEROULD

DARTMOUTH COLLEGE

THERE is perhaps no phenomenon of greater general interest to students of organic evolution than polymorphism, yet, although it is of frequent occurrence in insects, in few cases has it been investigated with long-continued and thorough experiments in breeding. Entomologists have usually been content to prove that different forms arise from the eggs of a single female, or of similar females of the same species, without reference to the male parent or to the immediate ancestors of the female. The time has come when these interesting phenomena, lying at the very doors of those at least who live in the country, demand more serious attention than they have yet received.

Colias philodice, the common yellow butterfly of the clover, called sometimes the clouded sulphur or roadside butterfly, is distinctly dimorphic in the female sex, in that the ground color of the wings is either yellow or white, the yellow female in most localities being much the more abundant. As this common species can readily be bred in large numbers, it affords excellent material for studying the inheritance of dimorphism limited to one sex.

[1] Read before the American Society of Naturalists, December 30, 1910.

Moreover the color pattern, which is the same in both the typical yellow and the albinic variety of the female, differs in the two sexes to such an extent that they may be distinguished even in flight. The wings of the

FIG. 1. *Colias philodice*. Male. FIG. 2. Yellow female.

male (Fig. 1) are marked with a solid black band of nearly uniform width extending along their outer margins, whereas in the female (Fig. 2) the marginal band is wider on the fore wings and usually invaded by spots

FIG. 3. White female.

of the ground color, but narrower on the hind wings and dusted with scales of yellow or, in the albinic variety, of white. The marginal band on the hind wings of the female in some individuals is absent altogether, the width of the bands in general in both sexes being very variable.

Besides these pronounced secondary sexual differences

in color and the common occurrence of the albinic female, a few specimens have been taken of an extremely rare mutation, the melanic male, in which the yellow is replaced by smoky black, the margin being distinctly paler than the ground color. In geographical distribution this aberration does not seem to follow the general rule laid down by Scudder that melanic forms occur in the southern part of the range of a species, for two of the specimens were from near Montreal, three seen and one captured at Palmyra, N. Y., and one now in the collection of Mr. H. P. Richardson, of Concord, Mass., was taken at Plainfield, Mass.

Partial melanism, or a melanistic tendency, often occurs in the female, though complete melanism has been found so far only in the male. This tendency reappears in successive generations independently of the environment, in certain strains that I have bred, though I think it possible that the action of the surroundings on certain individuals in a plastic condition may turn the germ cells in this direction. I have not yet had an opportunity to test this supposition, and my observations have been almost entirely directed to the inheritance of the albinic variety of the female.

Albinism in the genus *Colias* is due to the replacement of yellow pigment with another which is white (Fig. 3), all other pigments (black, red, etc.) remaining the same. The white is sometimes tinged with yellow, but there is a sharp difference between the color of a typical yellow female and that of the albinic form.

Albinism is not entirely confined to the females, though among the 900 descendants of white females that I have raised there has been not one white male. White males may be expected in regions where the white female is especially abundant. At Hanover, N. H., the proportion of white females to yellow is, perhaps, roughly five per cent. At Ithaca, N. Y., Professor Macgillivray informs me, the proportion of white females is considerably larger, being perhaps 10 or 15 per cent., and at Milton, Mass., Mr. W. L. W. Field estimates them at 20–25 per cent. In two localities where the white male has been

taken, about 50 per cent. of the females are white. These regions are Lava, Sullivan Co., N. Y., reported by Mr. Geo. Franck, and Alstead, N. H., on the authority of Mr. W. L. W. Field, who has seen only one white male, however, during several seasons of field work in that region.

Scudder makes the statement that "In the north this rarely, almost never, occurs in the first brood of the season, and is found much more abundantly in the latest than in the middle brood, the numbers increasing as the season advances." If this statement is true, it has an important bearing on the inheritance of the white character,[2] for he means, of course, that the proportions of the white females to yellow in the spring broods is less than in the later broods. My observations at Hanover in 1909, and those of my collaborator Mr. P. W. Whiting in Cambridge, Mass., in 1910, do not bear this out, for we found the white females in both places quite as common in the spring brood as in those of summer or autumn. Edwards likewise states that in the south the white form is not infrequent in the spring brood. The probable reason for Scudder's observation is that the population of the spring brood in the long run may be relatively small, because many of the hibernating caterpillars perish. The chances of finding white females in the field in the spring after a severe winter may therefore be less than during the flight of the more abundant summer broods that have not been affected by disastrous winter weather.

One of the most interesting observations that I have made during the past two seasons was the discovery of a wild female *Colias philodice* of the spring brood closely resembling *Colias nastes* of Labrador (Fig. 4), with a greenish-yellow field overspread with brownish scales, giving a grayish effect. In the margin brown replaces black. This form of female is not common, and I have seen it nowhere described. It was captured at Hanover, N. H., on June 10, 1909, and produced a brood of 34 butterflies (Fig. 5) of which 19 are males, all of which are yellow, 10 are yellow females, 5 are white females. The yellow and white colors of these offspring are of an

[2] See foot-note, pp. 266, 267.

unusually clear hue, and quite unlike the color of the mother.

The progeny of this female show that, supposing her to have mated with a pure yellow male not carrying white, as was probably the case, she is a heterozygote for

FIG. 4. The upper figure represents a spring form of female of *Colias philodice* from Hanover, N. H., resembling *C. nastes* of Labrador, shown in the lower figure.

color, potentially white, though modified probably by the effect of cold upon the chrysalis in early spring into a form strikingly like that of the Arctic species, *Colias nastes*. I hope to ascertain from caterpillars now hibernating whether this spring form may be produced at will from larvæ from a white mother by the action of cold upon the chrysalis.

My attention was attracted to the problem of inheritance of the white color in this species by certain statements in Edwards's great work on the "Butterflies of North America." He says that the progeny of an albino female are partly albino and partly yellow, or it may be all yellow. "In one instance," he says, "I had five butterflies from eggs laid by an albino, and there resulted one male and four yellow females, no albino.

In another case of four females one was an albino. Mr. Mead has met with similar results, and neither of us have known an albino to be produced from the eggs of a yellow female.'' These brief notes pointed

FIG. 5. The spring form of female of *Colias philodice* (at the top) and her offspring. The two rows at the bottom are yellow females; the third row from the bottom are white females. .None of the offspring resemble their *nastes*-like mother.

so clearly to Mendelian inheritance that I resolved to investigate the matter, and I have thus far bred over 900 individuals from white females and from the daughters and sons of white females. In general my results differ from Edwards's observations at two points: (1) The white females always produce both white and yellow females, provided the family is large enough to represent all the possibilities. The family mentioned by Edwards, four yellow females, no white, was too small to indicate

that the mother would produce no white offspring. (2) Yellow females under certain conditions do produce both yellow and white offspring. Thus the mothers of families "e," "f," "i," and "k," 1910, were yellow, producing, respectively: 13 white and 14 yellow daughters; 7 white and 5 yellow; 30 white and 14 yellow; 19 white and 19 yellow. The conditions under which these four yellow females produced white offspring were alike. The female and the brother with which she mated were in each case the immediate offspring of a white female, the male mate in each case being presumably heterozygous for color, y(w), the yellow female homozygous for that color, yy.

1. Inheritance of the White Female

Summary of Results

My observations, begun in the fall of 1908 and extending through the two following seasons, some of the same stock now being in hibernation, may be summarized as follows:

1. The white female, of which I have tested 13 individuals, is in all cases heterozygous for color, producing when crossed with a pure yellow male (wild, or her own brother), either equal numbers of white and of yellow female offspring, in accordance with Mendelian expectation (stock from Cambridge, Mass., families a, b, c, d, 1910), or twice as many yellow females as white (stock from Hanover, N. H., families a and c, 1909). The male offspring of a heterozygous white female are all yellow, though presumably one half are heterozygous, y(w), and one half homozygous dominants, yy.

2. It is evident from these observations that white is dominant in the female, yellow in the male, these being the colors of the respective heterozygotes. This case is comparable to the results obtained by Wood in crossing horned Dorset with hornless Suffolk sheep, the male heterozygote of F_1 having horns, the ewes being hornless. The horned condition is therefore dominant in the male, while in the female hornlessness is dominant.

TABLE I

WHITE ♀[4] [HETEROZYGOUS, w(y)] × YELLOW ♂ [HOMOZYGOUS, yy]

Mother	Father	Name of Brood	Number of Males	White Females	Yellow Females
Wild, white	Wild, yellow	1808	3	2	3
" "	" "	1909 a	39	7	16
Nastes-like form[5]	" "	" b	19	5	10
Wild, white	" "	" c	13	3	7
Total in 1908 and 1909			74 ♂♂	17 ♀♀	36 ♀♀

Mother	Father	Brood	Males	White Females	Yellow Females
Wild, white A	Wild, yellow	1910 a	18	6	9
" " B	" "	b	79	22	28
" " C	" "	c	24	8	8
" " D	" "	d	30	15	13
Total in 1910			151 ♂♂	51 ♀♀	58 ♀♀

3. If a heterozygous white female is crossed with certain other yellow males, her brothers and the sons of the same white female, that are heterozygous for color (as indicated by the fact that when mated with homozygous yellow females both white and yellow offspring result), a larger number of white females than of yellow are produced, though not three white to one yellow according to Mendelian expectation. The proportion observed is approximately two to one (viz., 38:22, 13:8, g and h, 1910, and probably the 8:4 of family 2w, 1909). This proportion may be explained, as Dr. Castle first suggested to me, by assuming that in these families no homozygous whites occur, through infertility or abortion of the "white" germ cells that would naturally combine with white, so that the offspring consist of:

♂♂ 25 per cent. homozygous yellow, yy, and 50 per cent. heterozygous yellow, y(w).

♀♀ 25 per cent. homozygous yellow, yy, and 50 per cent. heterozygous white, w(y), no pure homozygous whites of either sex occurring in my cultures.

[4] The sign ♀ stands in Tables I–VI for the white female, ♀ for the yellow female.

[5] This individual is possibly a pure yellow (yy) ♀, modified by cold and mated with a heterozygous y(w) male. It is possible that this brood should be included in Table IV.

TABLE II

WHITE ♀ [HETEROZYGOUS, W(Y)] × YELLOW ♂ [HETEROZYGOUS, Y(W)]

Mother (white)	Father (yellow)	Brood	Males	White Females	Yellow Females
1d[36]	*1d[8] ♂	l	4	3	3
1d[39]	†1d[18]	g	63	38	22
1d[45]	"	h	16	13	8
Total			83 ♂♂	54 ♀♀	33 ♀♀

TABLE III

WHITE ♀ [HETEROZYGOUS, W(Y)] × YELLOW ♂ [UNTESTED, YY OR Y(W)]

Mother (white)	Father (yellow)	Brood	Males (yellow)	Females (white)	Females (yellow)
a[35] ♀	a[6] ♂	1909, 2w	20	8	4
4b[21]	4b[15]	1910, m	9	5	3
1b[39]	1b[31]	o	9	3	4
Total			38 ♂♂	16 ♀♀	4 ♀♀

Thus here is a case comparable to that of yellow mice, which, as shown by Cuénot, Castle and others, are always heterozygous, homozygous yellow mice not being produced; so that the proportions obtained by mating yellow mice together is 66.6 per cent. yellow, 33.3 per cent. non-yellow.

4. The wild white males which occur rarely are presumably recessive homozygous whites, but none have yet appeared in my crosses of heterozygous yellow males with heterozygous white females (g and h, 1910), and I have not yet had an opportunity to test their possibilities in breeding.

TABLE IV

YELLOW ♀ [HOMOZYGOUS, YY] × YELLOW ♂ [HETEROZYGOUS, Y(W)]

Mother (yellow)	Father	Brood	Males	White Females	Yellow Females
a[14] ♀	a[7] ♂	1910, e	58	13	14
a[10]	a[19]	f	10	7	5
1d[30]	‡1d[8]	k	46	19	19
1d[46]	‡1d[18]	i	27	30	14
Total			141 ♂♂	69 ♀♀	52 ♀♀

* Tested by crossing with 1d[30] ♀ (yellow). See Table IV.
† Tested by crossing with 1d[46] ♀ (yellow). See Table IV.
‡ See Table II.

TABLE V

YELLOW ♀ [HOMOZYGOUS, yy] × YELLOW ♂ [HOMOZYGOUS, yy]

Mother (yellow)	Father	Brood	Males	White Females	Yellow Females
a^{24}	a^{6}, a^{23}, a^{26} or a^{42}	1909, 2y	20	0	15

Total number of males 507
Total number of females 412

TABLE VI

THE RESULTS OF BREEDING EIGHT DIFFERENT PURE LINES OF STOCK DURING 1908–1910. Brackets enclose designations of individuals used in subsequent breeding

Mother	Father	Brood	♂ ♂	White Females ♀ ♀	Yellow Females ♀ ♀
1908					
Wild, white	Wild, yellow	.....	3	2	3
1909					
A ♀♀	" "	1909 a	39[a^{6}♂, *et al.*]	7 [a^{35}♀]	16 [a^{24}♀]
a^{35} ♀♀	a^{6} ♂	2w	20	8	4
a^{24} ♀	Either a^{6}, a^{23}, a^{26} or a^{42}	2y	20	0	15
1909 B					
Nastes-like form	Wild, yellow	b	19	5	10
1909 C					
Wild, white	" "	c	13	3	7
1910 A					
Wild, white	" "	1910 a	18 [a^{7}, a^{19}]	6	9 [a^{14}♀, a^{10}♀]
a^{14} ♀	a^{7} ♂	e	58	13	14
a^{10} ♀	a^{19} ♂	f	10	7	5
1910 B					
Wild, white	Wild, yellow	b	79 [$4b^{15}$♂, $1b^{31}$♂]	22 [$4b^{21}$♀♀, $1b^{39}$♀♀]	28
$4b^{21}$ ♀♀	$4b^{15}$ ♂	m	9	5	3
$1b^{39}$ ♀♀	$1b^{31}$ ♂	o	9	3	4
1910 C					
Wild, white	Wild, yellow	c	24	8	8
1910 D					
Wild, white	" "	d	30 [$1d^{8}$, $1d^{18}$]	15 [$1d^{36}$, $1d^{39}$, $1d^{45}$]	13 [$1d^{30}$, $1d^{46}$]
$1d^{39}$ ♀♀	$1d^{18}$ ♂	g	63	38	22
$1d^{45}$ ♀♀	"	h	16	13	8
$1d^{46}$ ♀	"	i	27	30	14
$1d^{30}$ ♀	$1d^{8}$ ♂	k	46	19	19
$1d^{36}$ ♀♀	"	l	4	3	3

If the proportion of yellow females to white is really greater in the spring brood than in those of summer and especially autumn, as Scudder states, then it would be evident that some of the yellow females of the spring brood are heterozygous for color. See p. 260.

5. Yellow daughters of a white female are probably all homozygous for yellow.[3] When crossed with certain of their brothers, presumably heterozygous for color, these yellow females produce both yellow and white female offspring, sometimes in equal numbers, in accordance with Mendelian expectation (broods e, f, k), but sometimes twice as many white as yellow (brood i).

6. Yellow homozygous females, daughters of a white female, when mated with other brothers presumably homozygous produce only yellow offspring (brood 2y, 1909).

2. Inheritance in *Colias Edusa*

The numbers of typical orange and of white females of the European *Colias edusa* obtained by Frohawk (1901) from the eggs of four wild white females (var. *helice*), viz., 110 white ♀♀ (*helice*) and 125 orange ♀♀ (*edusa*) with 302 ♂♂, are in approximation to equality, and point to the conclusion that, in this species also, the white female is heterozygous for color.

Harrison and Main (1905) raised from the eggs of a white female (*helice*) of this species 79 ♂♂, 52 ♀♀ *helice* (white), and 19 ♀♀ *edusa* (orange). The numbers indicate that in this case both the parents were probably heterozygous for color. All the male offspring were of the typical orange hue, so it may be assumed that the 25 per cent. of homozygous white males that would be expected from mating two heterozygotes together were aborted, though the numbers indicate that 25 per cent. of the females were homozygous in whiteness. The expectation in the distribution of the observed number (71) of females would be

[3] It is of course not impossible that yellow females that are heterozygous for color may exist, and that this may account for the excess of yellow females over white in broods a, b and c, 1909. In order to test this matter and to determine whether, when a pair of yellows throw white, it is the male or the female that carries the white, the male crossed with any yellow should first be mated with a female known to be of a pure yellow strain. If such a pair throws only yellow, he is of course pure yellow, and if he is then paired with a yellow, and white offspring should appear, the occurrence of a yellow heterozygous female would be demonstrated, but if he has produced white offspring with a pure yellow female, he is assuredly a heterozygote, and will have some white daughters when paired with any yellow female.

$17\frac{3}{4}$ homozygous white, ww, $+35\frac{1}{2}$ heterozygous white, w(o), $+17\frac{3}{4}$ homozygous orange, oo, $=53\frac{1}{4}$ white [ww + w(o)] + $17\frac{3}{4}$ orange, which accords closely with the actual count, viz., 52 white (*helice*), 19 orange (*edusa*).

3. General Observations on the Genus *Colias*

Since the female color pattern is the one that prevails in both sexes when there is no differentiation (*e. g., Colias nastes, C. hyale,* etc.) I am inclined to the view that in this genus of butterflies at least, as probably in birds, the secondary sexual characters of the male represent a more highly modified, those of the female a more primitive, condition. We may recognize in this country, as in the eastern continent, a natural series of species of the genus *Colias,* at the beginning of which stands the undifferentiated Arctic *Colias nastes* of Labrador, Greenland, northern British America and Alaska, with the female color pattern, and a dull greenish yellow ground color suffused with brown, common to both sexes. This ground color, as my brood of *Colias philodice,* 1909, b, shows, is closely related to white and probably interchangeable with it. Next in the series are the subaretic *C. pelidne* and *C. scudderi,* in the males of which the yellow color and black color pattern typical of many species of *Colias* attain their full development, while all the females are clear white, with faint marginal dark bands.

The yellow ground color and the solid black marginal band probably arose by mutation in an undifferentiated *nastes*-like or white stock, and at once became dominant in the male, while the original colors and color pattern remained dominant in the female.

Southward from the range of *C. pelidne,* in the Canadian faunal region, is the closely related *C. interior,* in which yellow females (var. *laurentina*) occur, though white females are "on the whole commoner" according to Scudder, and from this region southward extends *C. philodice,* in which the yellow females generally are far more adundant than the white. Finally, the orange color of *C. eurytheme* of the central and western states, in

which species a most complicated polymorphism occurs, probably represents a stage in evolution beyond the yellow, as does also the black of the melanic male mutant of *Colias philodice.*

The view that the color and color pattern of the male butterfly diverge more widely from the typical coloration of the group to which the species belongs, than those of the female, though advocated by Darwin, 1871, was strenuously opposed by Scudder ('89, Vol. 1, p. 531), who cites the white female of *Colias philodice* as evidence to support his position. The case of *Argynnis diana,* in which the dark blue female differs much more widely from the usual tawny color of the fritillaries than does the male, certainly points strongly to Scudder's view, but it may well be that no one rule applies to all genera of butterflies, though there are in butterflies and in birds few if any exceptions to the law that the plumage of the male is more brilliantly colored and more highly differentiated than that of the female.

4. Inheritance in *Papilio memnon*

Jacobson's observations on the Javan butterfly *Papilio memnon,* in which there are three varieties of female, and the discussion of them by de Meijere, 1910, show that, as in *Colias,* the dominant form among the females is the one most unlike the male, viz., the brownish, tailed *Achates;* the form that is recessive in the female, as in *Colias* also, is the one most like the male, viz., the dark tailless *Laocoon.* The intermediate variety, *Agenor,* is heterozygous, epistatic to *Laocoon* but hypostatic to *Achates.* In the male the dark color, recessive in the female, is completely dominant.

Inspection of Jacobson's results leads one to believe that two, or probably three, pairs of unit characters are involved, and that not all of the individuals recognized as *Achates* or as *Agenor* are of the same gametic constitution. The remarkable fact brought out by Jacobson is that, in the various combinations made, only two of the three varieties of female were obtained in any one brood.

As a working hypothesis, I regard the dominant female

form (the brownish tailed *Achates*) as the original type, from which the tailless dark-colored male and the somewhat similar *Laocoon* have been derived by mutation, in the same way that the white color, dominant in the female but recessive in the male of *Colias*, may be postulated as the ancestral color in that genus.

5. Inheritance of Sex

Discussion of the inheritance of sex in *Colias philodice* at present must deal in part with unverified hypotheses, because I have not yet secured and tested white males nor, if they exist, homozygous white females. Since, however, all other possible combinations have been realized, these may now be reviewed, and tentative predictions made as to what progeny may be expected in the future from homozygous white stock in its various combinations.

Let us suppose that the male color pattern and all primary and secondary sexual characters of the male are dependent upon the presence of a "determiner" for which the male individual is a homozygous dominant (xx), while the female individual is heterozygous, one half of the gametes which it produces containing the determiner (x) and one half lacking it (o). Thus the gametic constitution of the female may be represented as xo, that of the male as xx.

Taking color into consideration, the nature of the pure yellow male may be represented by the symbol: yyxx, that of the pure yellow female as yyox. Furthermore, if yellow is dominant in the male, and white in the female the male heterozygote would be y(w) xx, while the white female would have the symbol w(y) ox. Such a white female, being heterozygous in both color and sex, may be further assumed to produce in equal numbers gametes of four kinds. This hypothesis will appear perhaps more firmly grounded if we imagine that both of the mitoses which give rise to the polar bodies are differential divisions, instead of one being an equation division and one a differential division, as is usually as-

sumed or demonstrated to be the case. The eggs of the white female are, accordingly, to be represented as follows: yx, yo, wx, wo; those of the yellow female: yx and yo. It is not necessary to assume in gametogenesis of the heterozygous white female of *Colias* any repulsion between one determiner and another resulting in a coupling such as is believed to occur in *Abraxas*. The determiner for yellow and that for white have equal chances of passing into a gamete with the male determiner or into one without it.

There are, of course, nine imaginable sets of combinations that would take place in the fertilization of the eggs of a species with three sorts of females: yyox, w(y)ox and wwox by the sperms of the males: yyxx, y(w)xx and wwxx. We will consider first the combinations that up to the present time actually have been made in my cultures.

1. THE PURE YELLOW FEMALE × THE PURE YELLOW MALE

yyox × yyxx

yx, yo = gametes of the female
yx, yx = gametes of the male

yyxx, yyox = 50 per cent. pure yellow ♂♂, 50 per cent. pure yellow ♀♀.
(Brood 2y, 1909.)

2. THE PURE YELLOW FEMALE × HETEROZYGOUS YELLOW MALE

yyox × y(w)xx

yx, yo = gametes of the female
yx, wx = gametes of the male

yyxx, yyox, y(w)xx, w(y)ox

25 per cent. pure yellow ♂♂, 25 per cent. pure yellow ♀♀, 25 per cent. heterozygous yellow ♂♂, 25 per cent. heterozygous white ♀♀, all the males being yellow, and the females yellow and white in equal numbers. **(Broods e, f, k, i.)**

3. WHITE HETEROZYGOUS FEMALE × PURE YELLOW MALE

w(y)ox × yyxx

wx, wo, yx, yo = gametes of the female
yx, yx = gametes of the male

y(w)xx, w(y)ox, yyxx, yyox

♂♂ 50 per cent. pure yellow, 50 per cent. heterozygous yellow,
♀♀ 50 per cent. pure yellow, 50 per cent. heterozygous white,
all the male being yellow, the females yellow and white in equal numbers. **(Broods a, c, 1909; a–d, 1910.)**

4. WHITE HETEROZYGOUS FEMALE × HETEROZYGOUS YELLOW MALE

$\overline{w}(y)ox \times y(w)xx$

wx, wo, yx, yo = gametes of the female
yx, wx = gametes of the male

y(w)xx, w(y)ox, yyxx, yyox

y(w)xx w(y)ox

wwxx wwox. Assuming that the last two combinations (homozygous whites) are cancelled, we should have:

♂♂ 25 per cent. pure yellow, 50 per cent. heterozygous yellow,
♀♀ 25 per cent. pure yellow, 50 per cent. heterozygous white.

This combination has also been accomplished in my cultures, *e. g.*, broods g and h, 1910.

The five possible remaining combinations may never be completely realized owing to partial or complete infertility of the homozygous white stock. However, white males do occur, and assuming that homozygous white zygotes might be successfully produced, the resulting combinations would be as follows:

5. PURE YELLOW FEMALE × HOMOZYGOUS WHITE MALE

yyox × wwxx

yx, yo = gametes of the female
wx, wx = gametes of the male

y(w)xx, w(y)ox, that is, both males and females would be heterozygous for color, all the males being yellow, all the females white.

6. HETEROZYGOUS WHITE FEMALE × HOMOZYGOUS WHITE MALE

w(y)ox × wwxx

wx, wo, yx, yo = gametes of the female
wx, wx = gametes of the male

wwxx, wwox, y(w)xx, w(y)ox, giving

♂♂ 50 per cent. heterozygous yellow, 50 per cent. homozygous white,
♀♀ 50 per cent. heterozygous white, 50 per cent. homozygous white,

thus all the females would be white, but the males yellow and white in equal numbers.

7. HOMOZYGOUS WHITE FEMALE × PURE YELLOW MALE

wwox × yyxx

wx, wo = gametes of the female
yx, yx = gametes of the male

y(w)xx, w(y)ox, or the males all heterozygous yellow, the females all heterozygous white [the same result as in (5)].

8. HOMOZYGOUS WHITE FEMALE × HETEROZYGOUS YELLOW MALE

wwox × y(w)xx

wx, wo = gametes of the female
yx, wx = gametes of the male

y(w)xx, w(y)ox, wwxx, wwox, or
♂♂ 50 per cent. yellow, heterozygous, 50 per cent. pure white,
♀♀ 50 per cent. white, heterozygous, 50 per cent. pure white.

9. HOMOZYGOUS WHITE FEMALE × HOMOZYGOUS WHITE MALE

wwox × wwxx

wx, wo = gametes of the female
wx, wx = gametes of the male

wwxx, wwox, or the males all homozygous white, the females all homozygous white.

That the germ cells in the white female, which I have shown to be heterozygous for color, and which is presumably also heterozygous for the sex determiner, are really segregated in oogenesis into four distinct groups is strongly indicated by the realization of the results of this hypothesis as shown in ¶¶ 3 and 4. In this segregation there is no real "coupling," the sex determiner (x) being equally distributed among the white and the yellow gametes, but the chances are also equal that any gamete may receive the x factor, and become a male zygote when fertilized, or lack it, and become on fertilization a female organism.

As would be expected, there are similarities between *Colias* and *Abraxas*[6] in the method of inheritance of the white female variety in each. The female in both is heterozygous for sex, producing in equal numbers eggs which give rise to males and to females when fertilized by the like sperms of the homozygous male. But there are striking differences between the two forms in inheritance, *e. g.*, the dominance of the type color in *Abraxas*, compared with its dominance in the male only in *Colias*, white being dominant in the female; females of the type form that are homozygous for color are found in *Colias*, but not in *Abraxas*, in which all the type females are heterozygous, just as are all the white females of *Colias* that have hitherto been bred. The segregation of the

[6] Doncaster, L., 1908, Rept. Evol. Committee Roy. Soc., IV, p. 53.

color and sex determiners in the *grossulariata* female and the white female *Colias*, both of which are heterozygous in these two respects, takes place presumably by quite different methods. Other differences or similarities will doubtless come to light when the white male of *Colias* is bred.

The notation which I have here used to express the gametic constitution of *Colias* applies equally well to *Abraxas*, assuming that maleness is dominant and that in gametogenesis of the heterozygote for color and sex, viz., the female *glossulariata*, GLOX, the male determiner, X, accompanies into one gamete the determiner for high color, G; while the determiner for the undeveloped color, L, is coupled with that for the undeveloped (female) sex, viz., O. This seems to me to be a more plausible way of expressing the combinations demanded by the results than that there is a "repulsion" between the determiner for femaleness (which is assumed in this view of the case to be dominant) and that for the dominant strong color, G, as suggested by Bateson and Punnett.

On the other hand, it is true that their assumption that in *Abraxas* the male is a homozygous recessive may be applied equally well to *Colias*. However, I am constrained to adopt the view that the male in both is a homozygous dominant for the following reason:

Dominance in the male postulates the presence in all the sperms and in half the eggs of a chemical substance which in double quantity in an oosperm so stimulates it that the male characters, both primary and secondary, one by one make their appearance; while in single quantity (introduced by the sperm only) a lesser stimulus is given, and the organism develops in lesser degree along different lines into the female form. This hypothesis carries within itself an "explanation," feeble though it be, of the male form and color pattern, as well as of those of the female. It is in harmony with the fact that the intenser color of the male butterfly or moth, generally, represents a more advanced condition in the evolution of pigment than the paler colors of the female.

If, on the other hand, following the interpretation of

Doncaster's results given by Bateson and Punnett, 1908, and by Castle, 1909, viz., that the male is recessive and the sperms contain no sex determiner, which is presumed to be present in half of the eggs only, then we must imagine that a single quantity of this determiner raises one oosperm to the female condition, while, in the entire absence of it, it is understood that another oosperm proceeds to the development of the frequently more complex organs and generally brighter colors of the male.

In using a modification of the convenient notation for sex-limited characters devised by Wilson and modified by Castle to express the parallelism between recent discoveries in cytology and Mendelian segregation, I do not wish to imply that the symbol X, as applied to *Colias*, refers to any sort of chromosome. Nor is there, so far as I know, any cytological evidence as to the dominance or recessiveness of the homozygous male condition in the possibly large class of cases like *Abraxas* and *Colias* in which the female is presumably heterozygous for the sex determiner.

As Castle, 1909, has shown, there are two categories of cases in sex inheritance: viz., (A) those in which the female is assumed to be a homozygous dominant for the sex-determining factor (XX), while the male is a heterozygote, producing two sorts of spermatozoa that are not only physiologically but presumably even morphologically different. This category is illustrated cytologically by the extreme case of *Anasa*, in which one set of sperms, the male-producing, contain only four chromosomes each, while the other, the female-producing, have five, the number characteristic of all the eggs. The second class of cases (B) is that including *Abraxas* and *Colias*, in which the peculiarities of their inheritance can be explained by assuming that the female is heterozygous for the differential sex factor, producing two types of eggs, one destined, when fertilized by the sperm of the homozygous male to produce only males, the other only females. Furthermore Castle, following Bateson and Punnett, 1908, regards maleness as recessive, the oosperm contain-

ing only one sex factor, viz., that brought in by the spermatozoon.

The field represented by class A has naturally been well explored by cytologists, for in spermatogenesis the odd chromosome was discovered, and there it is expected; moreover the study of spermatogenesis is attended with less difficulty than oogenesis. Hence comparatively few observers have paid any attention to the behavior of the chromosomes in the maturation of the egg, and cytological evidence of the occurrence of possibly dimorphic eggs in the second class of cases is lacking, though Balzer's 1908 observations on oogenesis in the sea-urchin, mentioned by Wilson, 1909 b, indicate that something may be done along this line.

The cytological evidence bearing upon the Lepidoptera, so far as it goes, however, indicates that the male is morphologically homozygous. There is no dimorphism of spermatozoa, the same number of chromosomes being found in all the spermatids. There is, however, a heterochromosome, interpreted by the various observers as a pair of equal idiochromosomes, associated with the plasmosome in the growth period. According to Dederer, 1907, and Cook, 1910, it ultimately becomes indistinguishable from the other chromosomes, though in the butterfly and the moth examined by Stevens, 1906, its large size made it visible through the maturation mitoses, in both of which it divides into equal parts. Thus, in the seven moths and one butterfly (*Euvanessa antiopa*) examined by these observers, there is cytological evidence, if the chromosome theory of sex determination be assumed, that the male is homozygous. Unfortunately we have no exact information, so far as I am aware, as to oogenesis in butterflies. If it should be shown that in Lepidoptera there is a visible dimorphism of ova as regards the number of chromosomes, the cytological interpretation of sex determination would receive an interesting and important confirmation.

If such visible dimorphism should be discovered, it would be most interesting to see what bearing it has, if any, upon the question whether the homozygous male is

dominant or recessive. If the latter be indicated, then we may find that a suitable designation of the gametes of *Abraxas* and *Colias* would be that suggested by Wilson, 1909 b, viz., for the male YY and for the female XY, Y being the small synaptic mate of X, which is the large odd "female-producing" chromosome.

On the other hand, if the male is dominant a state of affairs that is exactly the reverse might be expected, viz., an absence of a chromosome, or an abnormally small one, in half of the eggs would be the visible sign of future femaleness. If these conditions should be realized, we might be able to identify the "equal idiochromosomes" already found in the spermatogenesis of butterflies with my XX of the male, the corresponding chromosome in the male-producing type of egg being X, the female-producing ova either lacking the chromosome altogether or having one of reduced size.

Dr. Castle, in a recent letter to me, expressed the opinion that the well-known anabolic tendency of the female, especially in reproductive activities, renders it extremely probable, on the other hand, that the female-producing gamete in every case of disparity should have the larger chromatic equipment. This seems to me very plausible, and it may well be that the findings of cytology in reference to this question can never do more than demonstrate the presence of this constant anabolic tendency in the female-producing gametes. The appearance of the large X chromosome in the female-producing gamete of the Hemiptera may be, therefore, only the visible expression of a sex tendency already established, as Morgan's observations on the cytology of *Phylloxera* indicate.

But the demonstration of this anabolic tendency, even in the unfertilized gamete, does not mean necessarily the *presence* of a sex determiner that is absent or deficient in the male-producing gamete, and hence the *dominance* of femaleness. It is just as reasonable to assume that the constant katabolic tendency of the male, evinced possibly by deficiency in chromatin at the start and certainly by the presence of horns, high colors and elaborate plumage

in adult life in many animals, is due to the excess of some hormone in a gamete which thereby becomes male-producing, in other words, to a *dominance of maleness*. On the other hand, in the absence of such an excitant, the recessive condition of femaleness would result, with a constant tendency towards quiescence, towards the accumulation of reserves of food to nourish the offspring, and the absence in the adult of the brilliant colors, horns and all the well-known and highly specialized secondary sexual characters of the male.

If it should be proved that maleness is dominant in lepidoptera in which the female is sexually heterozygous, may it not be true, on the other hand, that femaleness is dominant in the forms in which the male is heterozygous for sex, as in Castle's class A?

I see no inconsistency in these two antithetic categories, but should expect to find in the latter either that the female, and not the male, is the more variable, active and progressive, as in the bee, or that, as in hemiptera, both sexes are in external appearance and in habits much alike.

In brief, I have tried to point out in this discussion that a different interpretation from that of Castle may be applied to the case of *Abraxas*, and of *Colias* also, viz., that these cases, and others that may fall into the same category, differ from those of the well-established class A of Castle in that one is the exact reverse of the other, the female in class A being a homozygous dominant for the sex determiner, whereas in class B the male is a homozygous dominant, and not a homozygous recessive as has hitherto been assumed. The view here set forth not only accounts for the facts of Mendelian inheritance in these two insects equally as well as the other, but has the added advantage of harmonizing with the facts regarding the secondary sexual characters in lepidoptera and birds.[7] The high colors and elaborate plumage of the

[7] The recent experiments of Goodale, however, described in the *Biological Bulletin*, Vol. 20, No. 1, December, 1910, show that the removal of the ovaries from the Rouen duck produces a gradual tendency toward the assumption of the male plumage which is not in accordance with the view that

male are dominant characters eventually produced in the adult, according to my view, by the presence in the oosperm of a double quantity of a male-producing enzyme or similar substance. This hypothesis does not depend upon cytology for its support, though it is not impossible that future discoveries in oogenesis may be found to be in harmony with it.

6. Dimorphs

If complete separation of the yellow- and the white-bearing gametes should fail to occur in the oogenesis of the white female of *Colias*, in the differential division of an oocyte destined after fertilization to become a female individual, then the right wings of the future butterfly might be white, the left yellow, or *vice versa*. Such an individual, captured by Mr. J. H. Rogers, Jr., of Medford, Mass., is figured in *Psyche*, Vol. X, Pl. X, Fig. 4. A similar specimen of *Colias edusa*, the right wings being white, is figured by Fitch, 1878, in the *Entomologist* (No. 178, pp. 49–61). Fitch shows also a female with the fore wings white and the hind wings yellow. A gynandromorph might be produced by similar failure in the separation of a gamete containing the sex determiner from one lacking it. Various combinations of color and sex are theoretically possible in one individual, if we assume that imperfect division of the gametes may occur in gametogenesis. The discovery of these combinations in nature, or their production by artificial disturbance of the ova, is well within the limits of possibility.

The production of a dimorph with one side yellow and one white is easily explained if we assume, for example, that the determiners for yellowness and for whiteness, after synapsis, reside in a single bivalent chromosome, which fails to divide differentially in oogenesis, but passes over bodily into one of the gametes, the egg. If

the male in birds owes his more brilliant plumage to the addition of something to the female type.

the first cleavage completes the differential division of the bivalent chromosome, instead of dividing it lengthwise, the right and left dimorphism is easily understood. Or we might postulate the suppression altogether of the differential oogenetic division of the egg of a white heterozygous, w(y), female of *C. philodice* which normally results in the separation of color potentials, but it is questionable whether under such conditions the egg would develop.

Again, the theory of Boveri, 1902, that a gynandromorph is produced if a spermatozoon (sperm nucleus) unites with one of the two nuclei in the two-cell stage, instead of with the original egg nucleus; or that of Morgan, 1907, that two sperms enter, one uniting with the egg nucleus and (in the bee) determining the female half, while the other gives rise to the male half, may be applied to these dimorphs. According to Boveri's view, for example, we have to assume in the case of *Colias* that a "white" sperm from a heterozygous yellow male enters a "yellow" egg containing no sex determiner, and after awaiting the precocious division of the egg nucleus, unites with one of the two nuclei thus produced, and determines the character of the white, or hybrid, half of the resulting female organism.

7. Precocity of the Males

Males of *Colias philodice,* as in certain other lepidoptera, not only appear in the fields earlier than the females in the spring, summer, and autumn broods, but also, in every family of this species that I have raised, a very large proportion of males emerge from the chrysalis early in the period during which eclosion takes place. Thus, as shown by Table VII, in brood a, 1909, 28 males emerged from the chrysalis at the beginning of the period of eclosion, while only 3 females emerged during the same time, and, of the first half of the brood to pupate, 26 proved to be males and only 5 females. In general, 82 per cent. of the first half of the four broods for which data are here presented to reach the pupal

stage were males, only 18 per cent. females. The remaining individuals of these four families, constituting the second half of each in reaching the pupal stage, were, on the other hand, largely females (66 per cent.), only 34 per cent. being males.

These facts led me to entertain the idea that the eggs which are to become males may be laid before the female-producing ova. To test this hypothesis, I segregated the successive batches of eggs laid by seven females in 1910, and reared the larvæ of each successive batch separately, to see if the lots laid first by each female would contain a larger proportion of males than those laid later. It will be seen from Table VII that in families b, c, d and e there was in each case a slightly larger proportion of male eggs in the first laying than in the batches laid subsequently, but in families g, i and k exactly the reverse is true, the last lots of eggs laid by each female (viz., 3g and 4g, 2i, and 3k and 4k) containing more males than females. It is evident, therefore, that the male-producing ova are not laid on the average earlier than those that are female-producing, but that the larval period of the male is shorter than that of the female.

In consequence of this fact it is not surprising to find that when a brood of caterpillars is exposed to any adverse conditions such as starvation, an excess of male butterflies, as Mrs. Treat long ago found, will result, for the simple reason that many females, exposed to adverse conditions during a longer period of growth than that of the males, have been eliminated, while the more precocious male caterpillars survive in greater numbers. This will explain, I believe, the excess of males in my cultures, 507, or 55 per cent. of the total number being males, 412, or 45 per cent. being females. There is no evidence, however, of any differential death rate between the yellow and the white females. Neither is more precocious in larval development than the other, and intestinal diseases appear to strike each with equal virulence.

TABLE VII

PRECOCITY OF MALES IN *Colias philodice*

Year	Brood	First Half of Brood to Pupate ♂♂	First Half of Brood to Pupate ♀♀	Dates of Pupation	Second Half to Pupate ♂♂	Second Half to Pupate ♀♀	Dates of Pupation	First Eclosion
1909	a	26	5	June 25–29	13	18	June 29–July 1	July 2-9 ♂♂ 28 ♀♀ 3
1909	b	14	3	July 2–4	5	12	July 4–6	
1909	c	10	1	July 7–10	3	9	July 11–13	
1910	a	13	4	July 9–13	5	11	July 13–19	
	Total	63 ♂♂	13 ♀♀		26 ♂♂	50 ♀♀		

Eighty-two per cent. of first half of all broods in reaching the pupal stage are males.

Thirty-four per cent. of the second half of broods in reaching the pupal stage are males.

Year	Brood	Males	Females	Per Cent. of Males	Brood	Males	Females	Per Cent. of Males
1910	1b	33	12	73 from 1st batch	1g	16	13	55
	2b	7	3	70 from 2d batch	2g	18	23	44
	3b	9	7	56 from 3d batch	3g	21	19	52.5
	4b	30	28	51.7from 4th batch	4g	8	5	61.5
	1c	20	13	60.6	1i	13	22	37
	2c	4	3	57	2i	14	22	38.8
	1d	12	10	54.5	1k	8	11	42
	2d	7	6	53.8	2k	15	12	55
	3d	11	12	47.8	3k	13	10	56.5
					4k	10	5	66.6
	1e	13	3	81.2				
	2e	18	12	60				
	3e	27	12	69				

These investigations are by no means finished, and any one who should chance to capture any unusual specimen of this species, or of any closely allied to it, showing melanistic or other aberrant tendencies, would confer a great favor on the writer of this paper by mailing to him the specimen alive in a metal box lined with moist filter paper sewed firmly against the perforated sides. A white male is, of course, especially desired.

In conclusion, the writer wishes to express his hearty thanks to his friend Mr. P. W. Whiting, an accomplished student of butterflies, for his kind and efficient cooperation in the field work connected with these studies and in the laborious processes of preparing specimens for detailed examination. The friendly counsel of Dr. W. E. Castle has been also of great value to the writer in

entering this to him new but extremely fascinating field of investigation.

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NUCLEUS AND CYTOPLASM IN HEREDITY[1]

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THAT there is a physico-chemical basis of heredity and that it is, if not exclusively, at least fundamentally bound up in the proteins of the germ-cells, we know for certain. If there is anything else than this physico-chemical basis we do not know it. But even should there be, it is inconceivable that it is not subject to physico-chemical agencies and limitations, and we are bound, therefore, to continue our search for these material factors as long as we can unearth new facts or arrive at new generalizations.

Before undertaking a discussion of the germ-cell, however, I wish to call attention to certain chemical facts that are frequently overlooked or slighted by the biologist.

In chemical reactions we have not only to take into account the initial chemical substances and such external factors as pressure, temperature, etc., but in many instances we must reckon also with the quantitative relations, especially the concentrations of the various substances, and the velocities of their reactions, since alterations in either of these factors may profoundly modify the end-products of the reactions. A very simple example of quantitative relations is seen in the combination of carbon and oxygen. If much oxygen is present, CO_2 is formed, if little CO, and these are two very different substances, particularly when physiologically considered. Or, when chlorine acts upon methane, CH_4, depending upon purely quantitative relations and physical conditions. any one of four different substitution products ranging from CH_3Cl to CCl_4 may be secured.

The questions of quantitative proportions and of velocities are of especially great significance in a sequence of

[1] Read before the American Society of Naturalists, at Ithaca, December 30, 1910.

reactions where a number of associated substances are concerned and where certain of the materials, before they can become active, must await the outcome of the reactions between other members of the mixture. For example, when hydrochloric acid is passed into an alcoholic solution of hydrocyanic acid, provided there are sufficient quantities of these three ingredients, five definite crystalline end-products of their interaction result. First the hydrochloric and hydrocyanic acids combine to form amido-formyl-chloride, which then adds another molecule of hydrocyanic acid. This product next reacts with one molecule of alcohol which to this point has been inactive. The result is what we may call end-product one. Then end-products two, three and four, respectively, are formed by the successive additions of a single molecule of alcohol to separate molecules of a part of the immediately preceding end-products. The fifth end-product is not so directly related to the others. It is elaborated chiefly through the interaction of hydrocyanic acid and water, but this interaction can not take place until water is released through dehydration of some of the other compounds. There is little doubt that such sequential reactions as these may be taken as simple models of what goes on on a tremendous scale in the developing germ-cell.

It is a well-known chemical fact, moreover, that when two or more progressive reactions are going on simultaneously, a quickening or retardation of the velocity of either, with the consequent precocious development of certain stages in the sequence, may lead to a partial or complete deflection of the original trend of the reactions and the formation of entirely different end-products than would otherwise have resulted. And velocities may be varied greatly by such factors as temperature and catalytic agents.

But what has all this to do with the germ-cell? Simply this, the substance of the germ-cell, in so far as we know it, is of materials such as proteins, carbohydrates and fats which we have no reason for doubting are subject

to the same fundamental laws of chemical behavior whether they exist in living matter or in non-living matter. If in the comparatively simple cases of associated simultaneous reactions with which we are acquainted in non-living matter, relative velocities may so modify the results, we can readily realize of what tremendous importance regulation of this matter must become in living protoplasm where doubtless vast numbers of chemical reactions and interactions are going on at the same time. In fact, could we locate such a time regulating factor in the germ-cell it would seem that we had accomplished a long stride toward an understanding of the controling and coordinating mechanism which insures the appearance of just the proper substance at the right time in morphogenesis. It would constitute a qualitative as well as a quantitative regulator, for by determining quantity at any given time it determines what the next chemical reaction will be, and hence in the very doing of this, it necessarily conditions the chemical outcome of that reaction. As we have seen, temperature and catalytic agents are important factors in modifying the velocities of reactions in ordinary chemical processes, and inasmuch as under normal conditions of development the temperature factor is a fairly constant one, we are left to face the question as to whether in protoplasmic phenomena there is anything to correspond to catalyzers. Such substances we find in the enzymes.

While the method of enzyme activity is not positively known, the consensus of opinion of those who have studied them most seems to be that they act by catalysis. For instance, both catalyzers and enzymes are effective in very minute quantities; neither appears among the end-products of the substances acted upon, but exists independently and in exactly the same quantity as at the beginning of the reaction; external conditions such as temperature affect their activities similarly; and lastly, the rate, that is, the velocity of the reaction concerned, depends upon the amount of the catalyzer or enzyme present. When we have explained the phenomena of

catalysis, therefore, we have at the same time doubtless gone far toward explaining the action of enzymes.

We know that different ferments act differently on the same substance and that the same ferments may act on different substances within certain limits. To realize the truth of the first proposition we have only to compare the results of the butyric, the lactic and the alcoholic fermentations of grape sugar. As to examples of the same ferment acting on different substances, we may point to the fact that some varieties of yeast will act readily on *d*-fructose, *d*-glucose, and *d*-mannose. They will not act on *d*-galactose, however. Furthermore, none of the other known aldose hexoses and ketose hexoses are acted upon by yeasts. In the case of yeast, then, where a given enzyme acts on more than one substance, the molecular configuration of the respective substances must be closely similar. This seems to be a general rule. We do not find the proteolytic enzyme trypsin attacking anything but proteids, although it operates on different kinds of proteids. Even oxidizing ferments are not exceptions in this respect, for certain of them will yield oxidations in some compounds and not in others that are readily oxidizable under the influence of a different oxidizing ferment.

But granted that in living protoplasm ferments play the important rôle of velocity regulators and consequently of conditioners of both quantitative and qualitative results, where should we look for them in the germ-cell? It is now a matter of common knowledge that probably many ferments are closely associated with nuclear activity and presumably originate within the nucleus. The present tendency is to regard the dissolution of the nuclear membrane from time to time as a means of distributing substances to the cytoplasm. Particularly in the case of the germinal vesicle of the egg, upon dissolution of the membrane, there is a copious discharge of nuclear material into the cytoplasm, and one would naturally infer that this is in some way a preparation for the subsequent rapid differentiation which will occur.

Various observers have pointed out the predominant part played by the nucleus in intra-cellular oxidations, operating apparently by means of oxidases. R. S. Lillie has shown that in the indophenol reaction the colored oxidation products in such cells as red corpuscles, and those of liver and kidney, are deposited mainly in and around the nuclei. He further points out[2] that certain ferments exhibit the properties of nucleoproteids and that they are apparently concerned with later chemical changes in the protoplasm chiefly oxidative in nature. As far back as 1895 Wilson and Mathews[3] showed that in the first maturation division of the starfish egg much chromatin is set free in the cytoplasm. In 1902 Conklin[4] called particular attention to the escape of nuclear material into the cytoplasm upon dissolution of the nuclear membrane in the egg of *Crepidula,* remarking further upon the large proportion of chromatin that passes into the cytoplasm during every cell cycle, where seemingly it plays some important part in the subsequent changes of the latter. Likewise, F. R. Lillie,[5] in 1906, pointed out that an important part in the development of *Chaetopterus* is played apparently by the great quantities of a "residual substance" set free from the germinal vesicle. Lyon[6] in 1904 showed a rhythmic parallel between nuclear division and the production of carbon dioxide by the cleaving egg. And Mathews[7] in 1907 suggested as probable that the periodic disappearance of the nuclear membrane during mitosis brought about a distribution through the cytoplasm of oxidases which had been synthesized in the nucleus. Wieman[8] in 1910 has shown the existence of alternate phases of acidity and basicity in the process of yolk formation in *Leptinotarsa,* due to a succession of oxidation processes which occur in

[2] *Jour. Exp. Zool.,* Vol. V, pp. 379–428, 1908.
[3] *Jour. Morph.,* Vol. X, pp. 319–342, 1895.
[4] *Jour. Acad. Nat. Sci., Phila.,* Vol. XII, pp. 1–121, 1902.
[5] *Jour. Exp. Zool.,* Vol. III, pp. 163–268, 1906.
[6] *Am. Jour. Physiol.,* Vol. XI, pp. 52–58, 1904.
[7] *Am. Jour. Physiol.,* Vol. XVIII, pp. 89–111, 1907.
[8] *Jour. Morph.,* Vol. XXI, pp. 135–216, 1910.

the basic-staining food-stream as the result apparently of the discharge of oxidase from the nucleus into the cytoplasm of the egg. Again, it is of great significance that in the embryos of seeds the time of greatest fermentative activity in starches and other fermentable bodies coincides with that of maximum size of the nuclei. Many other significant facts might be adduced. but I wish merely to show that there is abudant evidence pointing to the nuclei of cells as sources of enzymes.

The idea that among other things the nucleus is concerned with enzymic activities in the cell, or, indeed, that the chromosomes themselves are sources of ferments, is by no means a new one. The last few years has seen a steadily increasing tendency to regard them as such. The latest and most outspoken suggestion of this nature, of which I am aware, is the argument that Montgomery,[9] brings forward in a recent paper. He says in part, "The relative constancy of chromatin mass in spermatocytes and spermatids of very different volumes speak strongly for its enzyme nature." Then after pointing out the relative constancy in size between the univalent components of spermatogonia and spermatocytes in *Euschistis* and reminding us of the well-known fact that, although the egg is many times greater than the sperm, the chromosomal contribution of each is the same in size and mass, he goes on to say that, "An enzyme possesses among other properties the power of engendering changes in its medium while still preserving a constant mass." And he continues, "Of all the larger cellular compounds that we know, the chromosomes agree most closely with this definition, and by reason of this constancy of mass alone might be considered enzyme masses."

My present thesis, however, while in harmony with all this, is yet different. It is rather just the complement of such a proposition as Montgomery's for it is an attempt to show reasons why there *must* be a nicely adjusted series of such substances in the germ-cells as enzymes.

In any epigenetic conception of the germ-cell—and this

[9] *Biol. Bul.*, Vol. XIX, pp. 1–17, 1910.

in greater or less degree seems to be the only plausible one to-day—we are forced, in explaining morphogenesis to postulate the existence of some time-, quantity- and quality-controlling mechanism. The one evident class of substances in the germ-cells which can fulfil the necessities of the case are the ferments. For since they will determine the velocities of chemical reactions they must in consequence control the quantitative relations of the cell chemistry at any given unit of time. But from the very fact that where a large number of associated reactions are going on simultaneously, these quantitative relations at given stages of the chemical interchanges must profoundly influence qualitative results, we can not but conclude that this initial control of velocities must condition the qualitative results.

If we regard the chromosomes as centers of such a series of velocity-controllers, or, in other words, as sources of various enzymes, we can at once appreciate the necessity for having them so accurately balanced off in size and particularly in their quantitative relations one to another. For since the velocity of the reaction in a fermentable substance is determined not only by the presence of the ferment, but also by the amount of it, the quantitative relations of the ferments to one another would have to be very accurately maintained.

What appears to be in a way a non-chromosomal demonstration of this fact is found in connection with the chloroplasts of plant cells which seem to exercise their functions at least in part through the agency of ferments. As is well known, in cell division these bodies are each carefully divided and handed on to the daughter cells so that a constancy in number and in general relationships is maintained.

But, it may be objected, what is to be done with those cases of nuclear division in which the mitotic divisions of the germ-cells have been preceded by a series of amitotic divisions? Wieman[10] has shown that in amitosis the appearance of the division figures is by no means the

[10] *Loc. cit.*

same in all cases and that where it occurs among germ-cells the mechanism is more carefully adjusted than elsewhere. To quote his own words regarding such divisions in *Leptinotarsa*, "Thus in the oögonia and spermatogonia, division of the nucleus is preceded by a very exact division of a large chromatin nucleolus, and as the halves separate surrounded by a clear area, the appearance reminds one very much of the division of a chromosome on a spindle." Other investigators of such amitosis depict in their figures a mechanism which may have the same significance. From preparations of my own showing amitosis in the testes of snails and of *Planaria*, a similar interpretation could be given.

On this enzyme conception, however, constancy in number is not the fundamental necessity. The requirement is really constancy of equilibrium between chromosomal constituents. It matters not whether this is maintained in sixteen, eight, four or one chromosome, so long as the balance between the various enzymic foci, or the capacity for the restoration of such a balance, is maintained. The ultimate karyokinetic divisions of such germ-cells as earlier divide amitotically would seem to be the restitution of such a balance so that the proper quantitative conditions exist in the finished germ-cell. Wieman would account for the appearance of amitosis in early germ-cells on the ground of a reduced oxygen supply in each individual cell, consequent upon a very rapid increase in cell multiplication. All that is demanded in the enzymic conception which I am presenting is the preservation in some way of the general tension of equilibrium so that each enzymic focus can resume its customary activities when the occasion demands, or, to express it less teleologically, when the occasion permits.

This conception would seem all the more tenable since we have had to discard the idea of the continuance of actual chromosomal individuality in favor of that of their genetic continuity as expressed by Wilson. The

demonstration by Bonnevie,[11] that while the identity of the old chromosome is lost in the resting nucleus, nevertheless, each new chromosome arises by a kind of endogenous formation from within the substance of its immediate predecessor, is a good point in evidence. That mere number of chromosomes is not of fundamental importance is evidenced by the considerable number of known cases in which closely related species may be characterized by a considerable difference in the number of chromosomes. In my own researches on man and certain birds, I have shown that instead of eight, the expected number of chromosomes in spermatocytes of the second order, only four (disregarding the accessory which may be present) appear, but that they are apparently bivalent in nature.

As associated with embryonic development we should have to suppose that there are considerable numbers of these initial ferments, which, however, need not all be present in an active condition. Certain ones required for the first stages of development might well be supposed in the course of their activities to produce or free others, or activate them at the proper time to take up their part in the progressive chemical activities of development. It is probable, too, that many of the ferments of the fully developed organism peculiar to the special tissues have not existed as such in the germ-cell at all, but have arisen at a later stage in the cells they occupy as the outcome of the metabolic activities of the tissue cell itself. It is a current belief, indeed, that each kind of cell has its own specific ferments whereby it shapes up from the common food supply submitted to it in the lymph the substances necessary for its own intramolecular assimilation. Many intracellular enzymes are now known to exist and it is probable that proteolytic enzymes at least are found within the cells of all living tissues. This is demonstrated by the fact of autolysis, or the self-digestion of living tissues which

[11] *Arch. Zellforsch.*, Bd. I, pp. 450–514, 1908.

have been taken from the body under perfectly aseptic conditions and kept suitably warm and moist.

There is no obstacle in the way of supposing, furthermore, that if we regard ferments as of nuclear origin, the cytoplasm of a given tissue may not modify the ferment, as it itself takes on the necessary modifications for its own specific functions. We have good evidence that the production of ferments can be modified by even the substratum on which living organisms grow, and such a relation as this, close as it is, is certainly less intimate than that existing between nucleus and cytoplasm. For example, molds cultivated upon starch form diastase, but if provided with albumin they will produce instead a proteolytic ferment. Moreover, by gradually altering their other nutriments, yeasts can be made to utilize after a time various foreign compounds.

But granted the necessity of some such set of controllers as the enzymes, and locating them in the chromosomes of the germ-cells, does this not commit us to a rigidly chromosomal theory of heredity? By no means. If, as all evidence indicates, ferments operate as catalyzers, then we must not forget that it is the very general belief among chemists that catalytic agents do not initiate the chemical reactions with which we find them associated, but that they only tremendously accelerate such reactions, or in a few known instances retard them. Since the nature of the building material must determine fundamentally the nature of the thing built, we must look outside the enzymes for much that will determine the peculiar individual outcome of the developmental processes. Leaving out of consideration for the present other functions the chromosomes may subserve, we might regard them as a sort of gauge for the feeding out of enzymes at the proper rate to bring about proper velocity reactions in the other cellular constituents, and perhaps regard the whole matter of mitosis and exactness in chromosomal distribution as a mechanism by which a quantitative metabolic regulation is maintained.

But because chromosomal influences can regulate the

activity of other cellular constituents, there is no warrant for jumping to the conclusion that they are essentially more important than these other constituents. I may repeat in this connection what I have had occasion to say by way of reminder in a former paper, "A germ-cell in fact should need no special units to generate the peculiar *genre* equilibrium or idiosyncrasy of protoplasm which is distinctive of a particular kind of individual, since such a germ-cell not only is itself already an individual, but from the very fact of having had the same racial history as other individuals of its peculiar kind (be they germ-cell, embryo or adult) it must likewise as a whole already possess this distinctive idiosyncrasy." That is, the individual proteids of germ-cells—globulins, albumins, nucleoproteids and the like—bear from the very start the stamp of individual peculiarity, wherever they may reside in the cell. And since they constitute at least part of the materials which transform and interact and have their actions modified by enzymes, certainly they as much as the enzymes are responsible for the outcome.

Regarding the specificity of corresponding proteins in relation to the natural kinships of living organisms, some very interesting facts are brought to light in the recent voluminous and painstaking researches of Reichert and Brown.[12] They show, for instance, that in hæmoglobin, one of the few crystallizable proteins, the crystals of each species of any genus, while possessing a constant individuality, all belong to the same crystallographic system and generally to the same crystallographic group of the system. These authors further point out the fact that this isomorphism must signify in all probability correspondence in the fundamental chemical constitution and molecular configuration of respective hæmoglobins. In case of the individual species the difference in the characters of the crystals was found to be as great as with ordinary chemical salts or minerals that belong to an isomorphous group. One is seemingly

[12] *Univ. Cincinnati Studies*, September–October, pp. 1–19, 1909.

justified, therefore, in inferring from these results that the differences between corresponding proteins in different species of a genus are rather to be referred to differences in molecular configuration than in atomic composition of the molecule.

The case of hæmoglobin is only one of several lines of evidence that might be brought forward as indicating the specificity of proteins. The serum-albumins which constitute the very font of the living molecules of higher animals, differ very decidedly in different species in the readiness with which they crystallize. Or, a foreign serum-albumin injected into the veins of an animal of different species can not take the place of the corresponding albumin of the blood of that species, but acts rather as a poison and is quickly eliminated by the kidneys. Lastly, not unduly to multiply examples of protein specificity, may be cited the precipitins which as you know may in general be used to show the degree of relationship of allied forms. For instance, when the blood-serum of one species of animal, let us say man, is injected at intervals into some other species, *e. g.*, the rabbit, the serum of the latter acquires the property of producing a precipitate in the serum of the first species, man in this case, but not in the serum of other animals unless they are relatively closely related to the first species. Thus the serum taken from rabbit's blood after a series of treatments with human blood will produce precipitation in the blood from any human being. It will produce some, though less, precipitation in the blood of the anthropoid apes, still less in monkeys, and none at all in animals distantly related to man. This implies, manifestly, that the more akin forms are, the more nearly identical are their proteins. And from the evidence brought forward in connection with the hæmoglobins we have seen that we are perhaps justified in regarding the differences between the proteins of closely allied forms as ones of molecular configuration rather than of molecular composition or constitution.

The question may arise in some minds as to whether

there could be sufficient number of configurational differences in the corresponding protein molecules of different species to account for the specificity of the respective proteins. When, however, we consider that to the serum-albumin molecule alone—and it is by no means the most complex protein—estimates assign the capability of having as many as ten thousand million stereoisomers, there would seem to be in this factor of configuration alone ample possibilities for the necessities of the case.

Because of imperfect methods it has in the past been well nigh impossible to tell how nearly chemically identical corresponding proteins of different species are. Reichert and Brown[13] point out that what formerly passed current as difference in composition may have been due in reality to contaminations or mixtures. "For instance," they go on to say, "the fact that the egg-white of the egg of certain species remains perfectly clear upon boiling, while that of other species becomes opaque, might be taken as meaning a difference in chemical composition, but the difference has been shown to lie in the different amounts of alkali and saline present." Again, "The centesimal analysis of corresponding albumins and globulins have failed to show any positive differences. Oppenheimer states, from the results of a recent study of serum-albumins of man, the horse and the ox, that serum-albumin is a uniform and specific substance, and that the elementary analyses point to one serum-albumin." This would leave the matter of specificity to be explained solely on the basis of molecular configuration.

This brings up the whole question of protein constitution and configuration. While this is still pretty much a terra incognita still many interesting facts have come to light, and all of them point to the conclusion that we are in no wise compelled to regard the proteins as out-

[13] "The Differentiation and Specificity of Corresponding Proteins and other Vital Substances in Relation to Biological Classification and Organic Evolution: The Crystallography of Hemoglobins," Publication No. 116, Carnegie Institution of Washington, pp. 1–338, 100 plates, 1909.

side the pale of the well-known principles of constitution, polymerization, stereometry and the like which are known to obtain in simpler organic compounds such as the "ring" compounds or aromatic series, and the straight chain or aliphatic series.

It is a familiar fact that the native proteins are readily broken down through hydrolysis into simpler bodies which still possess protein characteristics. We may in fact either artificially or in normal digestion get a whole series of stages ranging from complex native proteins to simpler and simpler products. The sequence runs approximately as follows:

Proteins.
—Meta- or infra-proteins.
—Proteoses.
—Peptones.
—Polypeptids (a relatively small number of amino-acids linked together).
—Individual amino-acids.

Three fourths of the albumin molecule, for example, may be made to yield members of the large group of amino-acids.

Because of the great abundance of these bodies, and because of their universal presence as degradation products of proteins, the conclusion was reached that the protein molecule is essentially built up by a linking together of amino-acid molecules. This suggested the idea that by bringing about such linkage it might be possible to build up molecules of the protein type. To those who are familiar with the recent developments of physiological chemistry, the fact that the first steps toward this end have already been accomplished is well known. Some seven or eight of the amino-acids (leucin, tyrosin, glycocoll, alanin, aspartic acid, phenyl-alanin, and amido-valerianic acid) had already been produced synthetically before Emil Fischer began his work. Fischer and his pupils have synthesized over twenty new members. But what is still more significant, they

succeeded in securing linkages of certain ones of these, thus producing polymeric amino-acid compounds called by Fischer polypeptids. Bodies of this same type have been isolated from natural organic substances. These polypeptids resemble peptones in appearance and, moreover, they react in the same way peptones do toward enzymes and various test reagents. One of the artificially synthesized polypeptids, furthermore, is apparently identical with one of the known polypeptids found in digestion, and *l*-leucyl-triglycyl-*l*-tyrosin, when prepared artificially, seems to have all the properties of the albumoses.

The amino-acids possess both acid and basic properties. It is this amphoteric condition that renders linkage possible. The individual amino-acids which constitute the units in such polymerizations are frequently spoken of as "nuclei." Linkage has been obtained not only between similar "nuclei," but also between "nuclei" of different amino-acids.

The results point clearly to the conclusion that the peptones and higher proteins are huge molecules formed chiefly of amino-acid molecules linked together by NH and CO affinities left unsatisfied as a result of processes comparable to dehydration. Such a protein molecule may perhaps be represented as a main chain or ring, of which the respective links are amino-acid "nuclei." Glycocoll, NH_2CH_2COOH, for instance, would through dehydration have for its nucleus in such a chain $\text{—}NH.CH_2.CO\text{—}$. Furthermore, since one H of the CH_2 of such "nuclei"

$$(e.\ g.,\ \text{—NH.}\underset{\displaystyle \text{H}}{\underset{|}{\text{CH}}}\text{.CO—})$$

can be substituted by various compounds (acetic acid, buthane, methylparaoxybenzene, etc.) we are led to conclude that to each link of the protein chain, a side-chain, differing in constitution in different cases, is attached or is attachable by replacement of this hydrogen atom. The well-known instability of living protein would seem

to be due to the fact that the chemical systems in such a giant molecule are never fully saturated at any one time, so that there is continually an adding and detaching and shifting of side-chains with perhaps at times more fundamental shifts or replacements in the amino-acid "nuclei" themselves. Quantitative and qualitative differences of proteins would seem to depend fundamentally on the kind and amount of the constituent amino-acids and secondarily on the chemical nature of the various side-chains.

Probably the scheme as outlined is much simpler than the true conditions in the protein molecule, but it will serve as a sort of diagram of the relations which exist there. It is probable, too, that the conditions in different proteins vary greatly in complexity. The chief point to be emphasized is the fact that the results of many investigators bear out this general conception of the protein molecule.

It would seem then that in the light of our knowledge of the complex molecular configuration of the proteins, the substances which appear to be the most intimately concerned with life phenomena, we have, without resorting to the idea of mysterious separate entities, ample basis for that peculiar handing on of metabolic energies already established which we term *heredity*. The mechanism of heredity would seem to be not so much a local problem of nucleus or cytoplasm as of (1) fundamental species substances, probably mainly protein in nature, together with (2) equally specific enzymic substances which regulate the sequences of the various chemical and physical processes incident to development. As development progresses, more and more kinds of chemical products are released and in consequence an increasing number of chemical reactions are set going. After the germ becomes multicellular such new factors must be reckoned with as the influences, mechanical, chemical, etc., of the various parts of the body on one another. And even with our present meager knowledge of hormones we can see that this may be no inconsiderable factor in modifying the developing organs in complex organisms.

Looked at this way, the physical basis of heredity could not be considered a series of equipotent units, but rather it must be regarded as being composed of systems of units of different orders of organization and different degrees of coordination. Alterations in the configuration, constitution or relative positions of the unit constituents which represent the links of the main protein chain or ring, for instance, would precipitate much deeper-seated changes than would replacement of side-chains by those of different type, and such replacements would, in turn, doubtless appear objectively as differences of greater degree than those resulting from shifts in the composition or configuration of the individual side-chains.

Our whole scheme of natural classification, in fact, demands just such a physical basis as is depicted for the structure of the protein molecule. For morphological characters are not all equivalent. In any large group certain characters are more conservative than others and represent more fully the organization, as a whole, while in successive subsidiary groups the characters grade down to less and less inclusive ones until the trivial features which make up species differences and varietal traits are reached. However, this parallel between the make-up of the protein molecule and the natural classification of living organisms can be looked on only as a suggestive illustration because in addition to proteins other things often enter into the construction of what we term characters in plants and animals. These characters, indeed, are frequently blends of the effects of numerous influences.

But as an example of how changes in different parts of the protein molecule might work out visibly in the organism let us see how such alterations actually work out in simpler and better known compounds. In the familiar benzene ring compounds, for example, there exists (1) the main framework or more stable component, the so-called ring itself, and (2) innumerable substitution groups which can be attached to the "ring"

at any one of six places. These substitution groups can be shifted or replaced indefinitely without disrupting the ring itself. Still different effects are obtainable by the union of one or more rings (generally still retaining some of the substitution groups) directly with one another, or through the intermediacy of a third element or radical. In the numerous coal-tar colors, the color, which is one of the most obvious "characters," does not lie as such in the benzene ring itself, but is determined by the radicals attached to the ring, and in certain groups perhaps, in part by the manner in which two or more rings are united. If, for instance, into a molecule of azobenzene a radical of the amido-group (NH_2) is introduced, a body is constructed which through salt formation yields a dye. If instead of the amido-group a hydroxyl group is introduced, the result is likewise a dye but one of different color. And so a large series of tints may be produced by varying the substitution groups which replace H in the principal molecule.

We have constantly increasing evidence, finding recent expression, for instance, in a paper of Morgan,[14] of a fundamental stereometrical condition of the egg-plasm. And F. R. Lillie[15] has suggested the possibility that a specific polarity and symmetry are characteristic of the ground substance common to all cells of the organism. Stereochemistry is based on the assumption that the combining forces of an atom act in certain definite directions in space. This same conception of orientation must be carried on to the more complex organic units, the stereometrical relations of which, in turn, are but the continued expression, under other conditions, of the original atomic combining forces. And this being true, it seems reasonable to look upon the whole organism as but the further expression of such elemental factors.

In view of the facts regarding the closeness of identity of corresponding proteins of nearly related species, we must conclude that between two individuals of the same

[14] *Loc. cit.*

[15] *Jour. Exp. Zool.*, Vol. IX, pp. 534–655, 1910.

species, set apart by mere differences of sex and minor traits, the basal protoplasmic stereometry and the fundamental proteid constitution must be in large measure identical, so that bi-parental inheritance, if extending to all the details it has been assumed to embrace, would be largely a matter of duplicating identical protoplasmic constituents. It is an obvious fact, however, that the egg contributes vastly more cytoplasm than the spermatozoon, and in consequence the developing organism is more maternal than paternal in origin. I have argued this point at some length in a former paper,[16] where I attempted to show that we are not justified in asserting that the entire quota of characters which go to make up a complete living organism are inherited from each parent equally, but that rather we must restrict our assertion of equal inheritance to the sexual and specific differences which top off, as it were, the more fundamental organismal features. I further pointed out that since the actual manifest physical things contributed equally by each parent were the chromosomes, we might legitimately look to them as the chief source of the factors which determine individual differences. We know that a single reduced or haploid set of chromosomes is sufficient for normal development, both from the fact of artificial parthenogenesis, and the fertilization of non-nucleated egg fragments; hence the egg must contain all the possibilities of a new organism. But the only *measurable* things contributed by the sperm-cell are the individual characters of the male line.

We may infer then that the chromosomes of both male and female origin work together on or with the other germinal contents of the fertilized egg, and these are predominantly of maternal origin. Or to phrase it as I have in a former paper:[17] "Nevertheless, we can see how the veneer of individual traits may be equally of maternal and paternal origin if, to express it crudely, we look upon cytoplasm and chromatin, respectively, as responsive

[16] *Science*, June 28, 1907, pp. 1006–1010.

[17] *Univ. Cincinnati Studies*, September–October, pp. 1–19, 1909.

mechanism and inciting agent, the character of the response depending both upon the constitution of the cytoplasm and the material (enzymes? nutritive substances?) emanating from the nucleus."

If we consider that the supplying of the proper amounts and kinds of ferments is one of the important functions of the chromosomes, then we may suppose that in biparental inheritance each set of chromosomes is operating, probably catalytically, on a series of fundamental cell constituents that are largely common to both lines of ancestry; and that slight constitutional or configurational differences in corresponding enzymes bring about individual differences such as we recognize in the adult. We have already seen that different ferments within certain limits may act on the same substance and yield different results; consequently, in the intrusion into the egg of slightly altered enzymes in the chromosomes of the male, we should expect corresponding structural modifications to result.

It is not the intention to imply, however, that all character changes must be chromosomal in origin. Any influence which could effect constitutional or configurational changes in other essential constituents of the germ-cell would doubtless produce corresponding alterations in the adult. It is probable that not only changes of nuclear origin are reflected on to the cytoplasm, but that, conversely, cytoplasmic alterations may affect the nuclear constituents, for we have already seen how even the substratum may modify the enzyme factors in entire organisms such as molds and yeasts. Furthermore, there is no reason apparent why if the differences, no matter how produced, are modifications in the fundamental constitution or stereometry of the material affected, they should not persist permanently in the new germ-cells.

It would seem, in fact, that in the permanent effects of such reciprocal influences as here depicted for nucleus and cytoplasm, we might be able to account in large measure for the accumulations which have step by step been grafted on to the primitive protoplasm in its epi-

genesis toward the complex conditions of to-day, or in other words, in its racial evolution. Moreover, it is conceivable upon this basis how in later stages of phylogeny, as new chemical configurations or new chemical substances were developed, some of these could bridge back into relations with more primitively established substances and thus bring about ontogenetic short-cuts in development, or how, on the other hand, these abridgments might result in part from alterations in the more primitive molecular configurations. Racial reversions would be interpretable, at least in part, on the ground of the suppression of recently added processes or materials rather than on the reassertion of independently existing germs which had become latent.

The question arises, does not the very fact of the exactness with which the chromosomes are divided show that they are of greater fundamental importance than the cytoplasmic substances? Such a conclusion does not necessarily follow. The cytoplasmic substances of concern in development exist in the unfertilized egg apparently largely in a neutral or relatively inactive condition. The requisites are that these cytoplasmic substances be of a certain constitution and that there be a certain minimum amount of each. As insuring the presence of this indispensable minimal quantity there probably exists more or less of a surplus, but a surplus of this kind would not necessarily alter the result, as on my supposition the necessary quantitative conditions which determine the directing of the chemical reactions in the developmental processes are not brought about in this initial resting substance, but in the products of its fermentation, and the quantity of these at any given unit of time will depend upon the quantity of the ferment. Thus it is evident that by having the series of ferments accurately apportioned as we seemingly do in the chromosome, there can be an adequate quantitative and therefore qualitative regulation of the chemical processes without the controller being considered of fundamentally greater importance than the substances controlled.

I do not wish to be understood as maintaining that the nucleus or the chromosomes have no other than enzymic functions. We know that the nucleus contains highly complex proteins and it would seem improbable that all of them are concerned exclusively with matters of fermentation. There is some evidence, however, that the ferments themselves may be of the nature of nucleoproteids. If this is true it is possible that under certain conditions they operate as ferments and under other conditions as building or other necessary materials. My chief desire has been, without entering into a discussion of the manifold functions the nucleus may perform, to point out one obviously necessary function, the control of velocities in cell chemistry, that is explicable on the basis of enzymic activities, and to bring forward reasons for inferring that these have their sources in the chromosomes.

In conclusion, then, recalling the fact of the inconceivable number of stereoisomers that the proteid molecule may possess, and the fact that to make up protoplasm diverse proteins, at least, and various enzymes probably themselves of proteid nature, are required, we would seem to possess in the chemistry of relatively known chemical substances in nucleus and cytoplasm an adequate basis for interpreting the mechanism of heredity without resorting to other more hypothetical entities.

Before we embrace out of the void such new phantoms as "psychoids" or "entelechies" is it not incumbent upon us to strive still further to expand our knowledge of protein constitution and configuration? In the meantime it would seem best to look upon the organism, whether germ-cell or adult, as but the expression of an extended cycle of processes which are due to the intrinsic properties of the chemical constituents of protoplasm. Such an attitude at least has the merit of keeping within hailing distance of tangible facts and processes.

A COMPARATIVE STUDY OF THE STRUCTURE OF THE PHOTOGENIC ORGANS OF CERTAIN AMERICAN LAMPYRIDÆ

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OF the great amount of work that has been done in the production of light by living forms, not a little has been devoted to the structure of the photogenic organs. The organs whose anatomy and histology have been the subject of most of the researches have been those of the Lampyridæ. Although perhaps twenty-five species of these widely distributed insects occur within the borders of the United States proper, but little work has been done on the anatomy and histology of their luminous organs. The late Dr. Wm. H. Seaman (1) made some observations on *Photinus pyralis,* the insect which is so common in the parks in Washington in the summer, and a near relative of the *pyralis, Photinus marginellus,* has been made the subject of an extensive study by Miss Townsend, at Cornell (2). Wielowiejski (4) mentions having studied two American species, but fails to give their names. With these exceptions, however, the American Lampyridæ seem to have been neglected in the matter of histologic studies of the photogenic organs. Of the foreign Lampyridæ which have been studied, the principal species are *Lampyris noctiluca, Phausis splendidula, Phosphænus hemipterus* and *Luciola italica,* all European species, and all belonging to different subgroups from each other and from the American insects. Many studies have also been made upon the cucuyo, *Pyrophorus noctilucus* Linn., the large tropical elaterid firefly.

It has been thought worth while, therefore, to attempt some further study of the photogenic organs of such species of Lampyridæ as are accessible here, having in view especially the determination of the similarities and differences between them and between them and other

species which had been studied previously. The two species most common here (Washington, D. C.) are *Photinus pyralis* Linn. and *Photuris pennsylvanica* Deg., and the majority of our studies have been made on them. The classification relationships between these insects and the others that have been studied may be seen from Oliver's recent catalogue (3). As already stated, *Photinus pyralis* had been studied to some extent by Seaman, and its near relative, *P. marginellus*, by Townsend, but so far as we have been able to find, no studies have been made on any species of *Photuris*.[1]

A large number of slides have been made, containing transverse, longitudinal and oblique sections of the two insects above mentioned, and a few transverse sections of *Photinus consanguineus*. With these slides comparative studies of the structure of the photogenic organs have been made. The most essential result of these studies is that in these three species the structure of the photogenic organs is practically identical, and very similar to that described for some of the other species of Lampyridæ which have been examined. Many of the drawings given by Townsend of the structures in *Photinus marginellus* may represent with equal faithfulness the corresponding structures in *Photinus pyralis* and *Photuris pennsylvanica;* our slides of *Photinus consanguineus* were not entirely satisfactory, but so far as could be seen, the structures in this insect are identical with those in its larger congener, *pyralis*.

In all three insects the luminous organ is divided into two distinct layers, the inner one being white and opaque, and serving as a reflector, and the outer being yellowish and translucent, and containing the actual photogenic mechanism. The photogenic organs, as brought out by prior studies, are penetrated from the interior of the insect outward, by innumerable tracheæ, which ramify and anastomose within the true photogenic tissue, and unite within, above the reflecting layer, to

[1] Since this was written, it has been noted that Watasé (9) made a few observations on the structures in *Photuris pennsylvanica*, but makes only a brief reference to them.

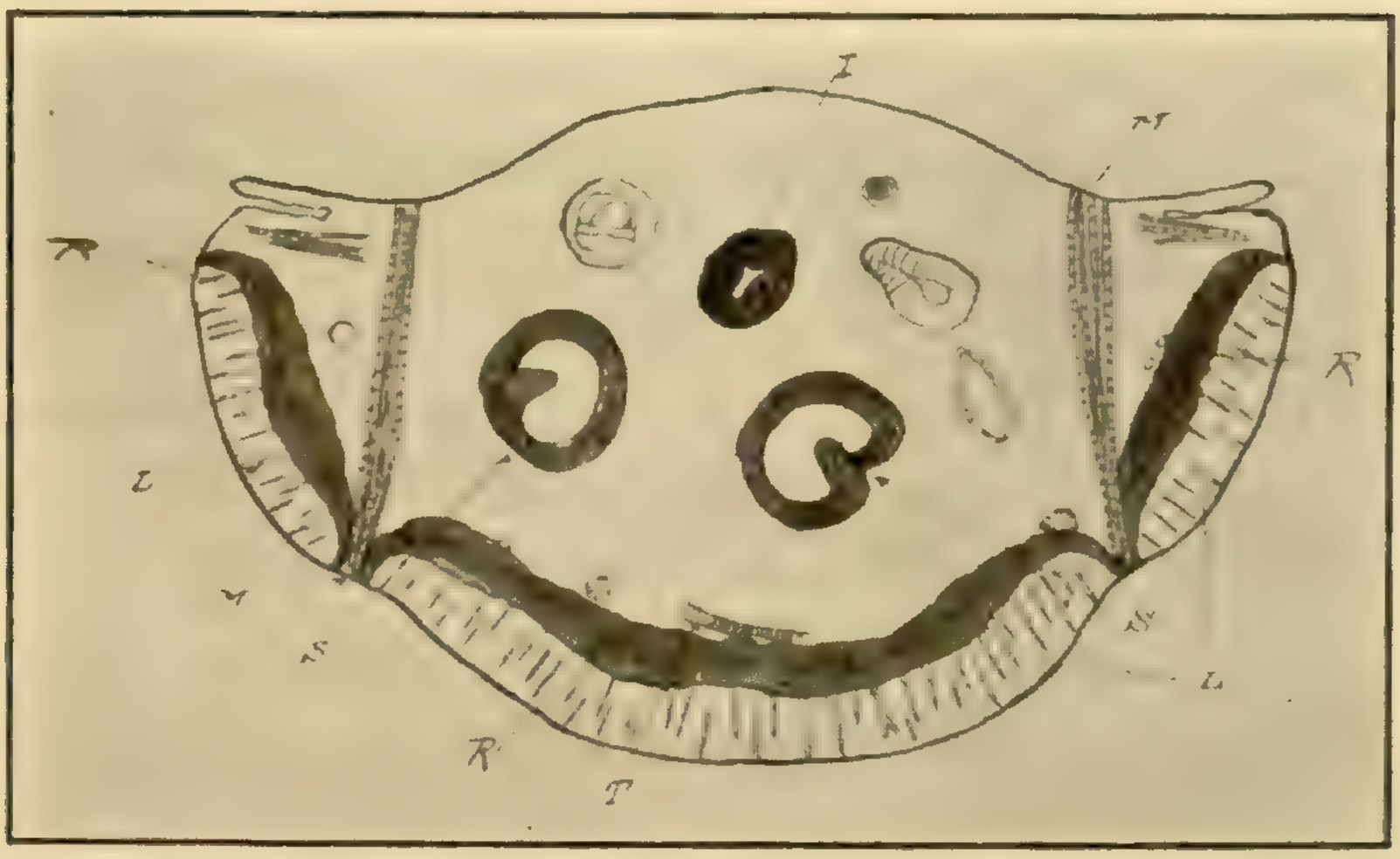

FIG. 1. Cross-sections at about the middle of the fifth abdominal segment of (*a*) *Photinus pyralis* and (*b*) *Photuris pennsylvanica*. *I*, intestine; *L*, photogenic tissue; *M*, muscle fibers; *R*, reflecting layer; *S*, spiral organs; *T*, tracheæ to photogenic organ.

form larger tracheæ; the latter lie nearly flat against the inside surface of this reflecting layer, and run diagonally outward, finally uniting almost at the spiracle with the breathing tracheæ, with which they are identical in appearance. The spiracles are on the dorsal side of the abdomen, one near either edge of each segment, and are furnished with some valvular arrangement at their orifice; the details of this structure have not yet been clearly made out. The arrangement of the smaller tracheæ and tracheoles is much the same in all three species. The tracheæ pass through the reflecting layer and the photogenic tissue perpendicularly to the surface. These tracheæ are furnished with chitinous hairs on the

interior as far as the point where they enter the reflecting layer; the presence of these hairs in tracheæ beyond this point and in the fine tracheoles, has not been observed. In their passage through the photogenic tissue, the tracheæ are surrounded by the structure referred to by Miss Townsend as the cylinder, a cylindrical mass of cells, sharply differentiated from those of the surround-

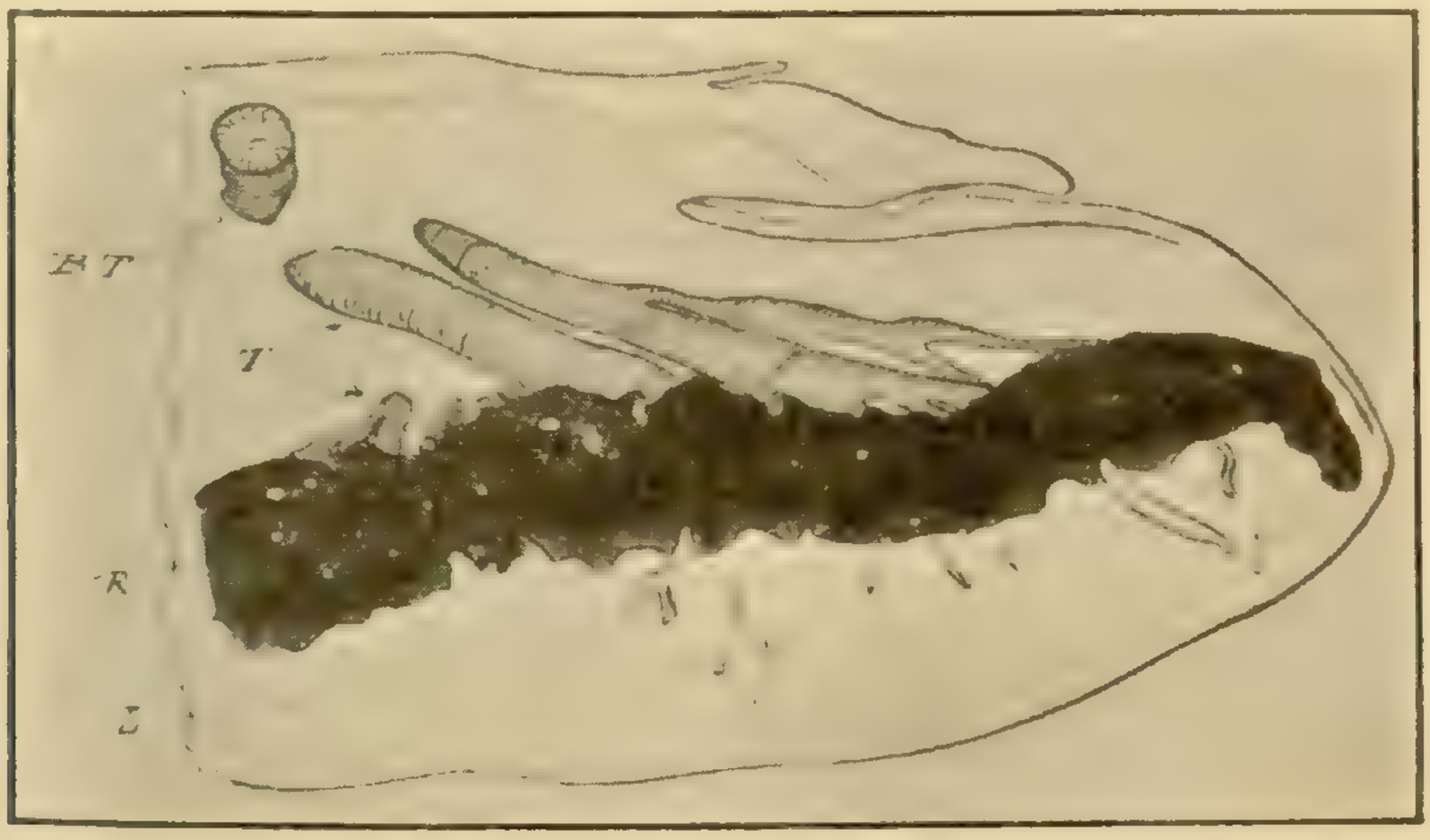

FIG. 2. Oblique section near edge of *Photinus pyralis*. *L*, photogenic tissue; *R*, reflecting layer; *T*, trachea to photogenic organ; *BT*, trachea leading to other organs. (Both of these figures are intended only as outline drawings, and no attempt has been made to show all the internal organs. or any great number of tracheæ.)

ing tissue, through which the trachea passes almost centrally. Within this cylinder the trachea throws off the numerous small branches, which at the edge of the cylinder break into the very fine tracheoles which pass into the photogenic tissue and anastomose between the cells with tracheoles from adjoining cylinders. The appearance of the large tracheæ above the luminous organ are shown in Fig. 2, drawn from an oblique section, the line of the cut being nearly parallel to the line of the larger tracheæ near the edge of the abdomen. At the lower end, just next to the superficial chitin covering the luminous segments, the main trachea subdivide into the large number of branches whose tracheoles radiate into the photogenic tissue, usually recurving slightly, so as to penetrate the tissue a short distance from the chitin.

The entire system suggests that the air is drawn in through the breathing tracheæ, and forced through the

fine passages in the true photogenic tissue, where the oxygen of the air is consumed in a biologic oxidation. In the sections of *pyralis* there are clearly seen bundles of muscle fibers on either side of the center line of the insect, which pass completely through the abdomen, almost vertically, and are attached to the exterior chitin at the top and bottom. At about the same point, other muscle fibers pass inward from the point of maximum width at each side; these fibers have not been traced to their full extent, but they appear to pass upward and toward the center near the dorsal side of the insect. These fibers are indicated in Fig. 1, *a*, at *M*. No similar muscle fibers have been observed in *Photuris*, although short lengths of muscle fiber passing vertically through the abdominal cavity have occasionally been noted, and these may be fragments of similar muscles to those in the Photinini. The corresponding muscles of *Photinus marginellus* are clearly shown in Fig. 1 of Miss Townsend's paper. Externally, the lower terminations of these bundles of muscle fibers appear as non-photogenic spots on the ventral surface of the luminous segments.

It may be well here to call attention to certain differences between *Photuris* and *Photinus*, as shown by the cross-sections of the insects. While there is a general similarity of outline in the cross-sections of the two species, the section of *Photuris* is generally a little flatter, and the ventral curvature of a somewhat larger mean radius, than in *Photinus*. Another difference has been very marked in our sections. While the thickness of the reflecting layer is about the same in both species, the layer of true photogenic tissue is much thinner, both actually and in comparison with the reflecting layer, in *Photuris* than in *Photinus;* this difference is clearly seen by reference to Fig. 1, *a* and *b*. This difference may be somewhat significant when considered in connection with the slight differences in the quality of the emitted light, and in the modes of emission of the two species. (See reference No. 8.) In *Photinus* there are two peculiar organs each consisting apparently of a thick-walled,

chitinous tube, coiled into a nearly cylindrical spiral, represented in partial section by *S*, *S*, in Fig. 1, *a;* these two organs appear to be glands which empty into a common duct which could be followed to the posterior extremity, and it seems possible that they are a portion of the male generative system, as they were not found in the female *pyralis,* although no spermatozoids were seen. The direction of rotation of the spiral was the reverse on the left side of the insect from that on the right. These organs were not found in the *Photuris,* although globular, glandular structures were found in approximately the same portion of the latter insect. This structure is shown in Fig. 2 of Miss Townsend's paper on *Photinus marginellus,* and in Fig. 1 of Seaman's (*Photinus pyralis*); the latter erroneously referred to it as the intestine; in our studies, the intestine of both *Photinus* and *Photuris* was seen as a nearly straight, thick-walled tube, indicated in section by *I* in *a* and *b* of Fig. 1.

The above remarks apply to the male insects. The two sexes in *Photuris* are almost indistinguishable externally; all those which we sectioned appeared to be males. In *Photinus pyralis,* however, the female differs markedly from the male. The luminous organ in the male occupies the entire ventral surface of the fifth and sixth segments of the abdomen, and the posterior portion of the fourth segment. In the female, the luminous apparatus is visible externally as a small, rectangular yellow spot, occupying about one third of the ventral area of the fifth segment of the abdomen. This organ obtains its air supply from a large trachea which extends along its forward edge, and apparently connects with the spiracles on the dorsal edges of the segment. In its finer structure, the photogenic organ of the female *pyralis* appears to be exactly like that of the male, as is to be expected.

That the photogenic process is an oxidation is scarcely to be doubted, in view of the work which has been done already. The work of one of us (McD.) with Professor

Joseph H. Kastle, of the University of Virginia, is of especial interest in this connection (6).

Our histologic methods presented no particularly new features. Most of our specimens were killed in hot 70 per cent. alcohol, stained entire in acid carmine, and mounted in paraffin. To secure proper penetration of the stain, it was found necessary to clip off the tip of the abdomen, or to slit the dorsal chitin. Osmic acid præparations were used a number of times, and in the sections of *Photinus consanguineus*, which were otherwise unsatisfactory, one per cent. osmic acid gave very good results for the fine tracheolar structure. For the study of the tissues under the dissecting microscope a good treatment was found to be to allow the detached, fresh luminous segments to soak in a mixture of equal parts of ten per cent. caustic soda and ten per cent. formaldehyde solution for three or four hours. This treatment left the tissues of both the reflecting and the active layers of the same gross appearance, though without entirely destroying the cellular structure; after being treated thus, the tracheæ and tracheoles can be seen as silvery white tubes and threads, on a background of dull, pale yellow, and may be followed down to the point of anastomosis.

It seems possible that the reflecting layer fulfils a two-fold purpose—that of reflecting the light outward, and thus increasing its intensity in the desired direction, and of protecting the insect itself from its own radiations. It has recently been shown by Coblentz (7) that the *pyralis* and other Lampyridæ contain a fluorescent material, and a number of observers have shown that fluorescent materials injected into a living animal show a higher degree of toxicity when the animal subsequently is exposed to light than if it be left in the dark.

To conclude: We have found that (*a*) the structure of the photogenic organs in *Photinus pyralis*, *Photinus consanguineus* and *Photuris pennsylvanica* is practically the same, and very similar to the structures of the corresponding organs in some of the other species of Lampyridæ that have been studied; (*b*) the tracheæ from

the photogenic organs connect near the breathing spiracle with the tracheæ which supply the other organs, and that they closely resemble the latter tracheæ in structure; (*c*) the view that the photogenic process is an oxidation is borne out by the structure of the photogenic organs.

We wish to express our appreciation of the assistance of Director John F. Anderson, of the hygienic laboratory, and Dr. Norman Roberts and Mr. Geo. F. Leonard, of that laboratory, and we are indebted to Dr. E. A. Schwarz and Mr. H. S. Barber, of the U. S. National Museum, for their kindness in supplying entomologic information, and to Professor W. A. Kepner, of the University of Virginia, for criticism and advice.

No attempt will be made here to give a complete list of the references to the literature of even the histology of the luminous tissues; so far as the latter branch of the subject is concerned, it is pretty thoroughly covered by the bibliography given by Miss Townsend, and the most complete bibliography yet published of the whole subject of physiologic light is contained in Mangold's extensive and interesting review cited as reference No. 5, below.

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4. Wielowiejski. Beiträge zur Kenntniss der Leuchtorgane der Insekten. *Zool. Anz.,* 1889, Vol. 12, pp. 594–600.
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8. McDermott. A Note on the Light-emission of some American Lampyridæ. *Canad. Entomol.,* 1910, Vol. 42, pp. 357–363.
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SHORTER ARTICLES AND DISCUSSION

A NEGLECTED PAPER ON NATURAL SELECTION IN THE ENGLISH SPARROW

In referring to Professor Bumpus's paper, "The Elimination of the Unfit as Illustrated by the Introduced Sparrow, *Passer domesticus*,"[1] as neglected, I do not intend to imply that it is unique in this respect. Several other important quantitative studies of natural selection, for instance papers by Weldon, Di Cesnola and Pearson, are in the same class. Indeed, the impression gained by reading papers commemorating the birth of Darwin and the publication of the "Origin of Species by Means of Natural Selection" is that the majority of biologists have little interest in natural selection as a scientific problem. The chief reason for this is probably the great development of experimental breeding during the last decade—a development which is a great source of satisfaction to biologists, but which has temporarily brought the study of evolution to a very one-sided stage of development.

At the time this lecture was published the statistical methods which are now considered the most suitable for dealing with such problems were not in the hands of many biologists. Recently in connection with some other work I had occasion to throw Dr. Bumpus's data[2] into statistical constants. These are published in the hope that they may suggest to some unoccupied biologist the collection of further quantitative data on the several problems presented by the introduced sparrow.

The characters dealt with are the following: (1) Total length in millimeters from tip of beak to tip of tail; (2) alar extent, the distance in millimeters from tip to tip of extended wings; (3) weight in grams; (4) length of head in millimeters from tip of beak to the occiput; (5) length of humerus in fractions of an inch; (6) length of femur in fractions of an inch; (7) length of tibio-tarsus in fractions of an inch; (8) width of skull in fractions of an inch; (9) length of sternum in fractions of an inch.

[1] Eleventh lecture before the Marine Biological Laboratory, Woods Hole, 1898; published in Biological Lectures from the Marine Biological Laboratory, 1898. Boston, Ginn and Co., 1899.

[2] Fortunately all the measurements were published.

Three classes of birds were distinguished—adult males, young males, and young and adult females.

We draw the following conclusions from the comparison of the means in Tables I–III with their probable errors.[3]

TABLE I

AVERAGES FOR ADULT MALES

Character	Survived	Perished	Difference
Total length.....	159.0571±.3154	162.0000±.3253	—2.9429±.4531
Alar extent.....	247.6857±.4333	247.3750±.4716	+ .3107±.6404
Weight (in grams)	25.4685±.1420	26.2708±.1966	— .8023±.2424
Beak and head.....	31.6143±.0709	31.6708±.0824	— .0565±.1095
Length, humerus ...	.7380±.0022	.7279±.0032	+ .0101±.0038
Length of femur.....	.7168±.0025	.7061±.0027	+ .0107±.0037
Tibio-tarsus.	1.1353±.0041	1.1202±.0051	+ .0151±.0065
Width of skull.....	.6025±.0016	.6033±.0017	— .0008±.0023
Keel of sternum.....	.8576±.0042	.8458±.0045	+ .0118±.0062

TABLE II

AVERAGES FOR YOUNG MALES

Character	Survived	Perished	Difference
Total length.....	159.6875±.4978	162.2499± .7291	—2.5624± .8828
Alar extent.....	246.8125±.7936	247.9167±1.2976	—1.1042±1.5213
Weight (in grams).	25.4938±.2040	26.2667± .3208	— .7729± .3801
Beak and head.....	31.8688±.1190	31.3249± .1138	+ .5439± .1646
Length, humerus....	.7416±.0039	.7347± .0055	+ .0069± .0067
Length of femur.....	.7162±.0046	.7153± .0050	+ .0009± .0068
Tibio-tarsus	1.1367±.0091	1.1393± .0071	— .0026± .0115
Width of skull.....	.6078±.0024	.5993± .0035	+ .0085± .0042
Keel of sternum	.8514±.0060	.8427± .0064	+ .0087± .0088

TABLE III

AVERAGES FOR ALL FEMALES

Character	Survived	Perished	Difference
Total length.....	157.3810±.4774	158.4286±.4859	—1.0476±.6811
Alar extent.....	241.0000±.6009	241.5714±.7142	— .5714±.9333
Weight (in grams)..	24.6190±.1531	25.3357±.2054	— .7167±.2561
Beak and head.....	31.4333±.1047	31.4786±.1068	— .0453±.1495
Length, humerus....	.7283±.0024	.7260±.0032	+ .0023±.0040
Length of femur.....	.7148±.0029	.7098±.0036	+ .0050±.0046
Tibio-tarsus	1.1436±.0042	1.1310±.0043	+ .0126±.0060
Width of skull.....	.6001±.0019	.6016±.0031	— .0015±.0036
Keel of sternum.....	.8193±.0043	.8207±.0037	— .0014±.0057

[3] For the individual comparisons those differences less than the probable error will be considered of no significance, those between one and two times their probable errors as possibly significant, and those over thrice their probable errors as probably significant.

TABLE IV

STANDARD DEVIATIONS FOR ADULT MALES

Character	Survived	Perished	Difference
Total length.....	2.7666±.2230	2.3629±.2300	+.4037±.3203
Alar extent.....	3.8005±.3064	3.4255±.3335	+.3750±.4529
Weight (in grams)..	1.2451±.1004	1.4276±.1390	—.1825±.1715
Beak and head.....	.6220±.0501	.5982±.0582	+.0238±.0768
Length, humerus....	.0196±.0016	.0230±.0022	—.0034±.0027
Length of femur.....	.0222±.0018	.0199±.0019	+.00 3±.0026
Tibio-tarsus.....	.0355±.0029	.0370±.0036	—.0015±.0046
Width of skull	.0317±.0011	.0123±.0012	+.0194±.0016
Keel of sternum	.0366±.0030	.0325±.0032	+.0041±.0044

TABLE V

STANDARD DEVIATIONS FOR YOUNG MALES

Character	Survived	Perished	Difference
Total length.....	2.9521±.3520	3.7444±.5155	— .7923± .6242
Alar extent.....	4.7066±.5612	6.6641±.9175	—1.9575±1.0755
Weight (in grams)..	1.2101±.1443	1.6474±.2268	— .4373± .2687
Beak and head.....	.7060±.0842	.5847±.0805	+ .1213± .1166
Length, humerus....	.0234±.0028	.0282±.0039	— .0048± .0048
Length of femur.....	.0272±.0032	.0258±.0035	+ .0014± .0047
Tibio-tarsus.....	.0537±.0064	.0365±.0050	+ .0172± .0081
Width of skull	.0141±.0017	.0180±.0025	— .0039± .0030
Keel of sternum	.0356±.0042	.0331±.0046	+ .0025± .0062

TABLE VI

STANDARD DEVIATIONS FOR ALL FEMALES

Character	Survived	Perished	Difference
Total length.....	3.2437±.3376	3.8119±.3436	— .5682±.4817
Alar extent.....	4.0825±.4249	5.6025±.5050	—1.5200±.6600
Weight (in grams)..	1.0400±.1082	1.6112±.1452	— .5712±.1811
Beak and head..	.7114±.0740	.8381±.0755	— .1267±.1054
Length, humerus....	.0160±.0017	.0255±.0023	— .0095±.0029
Length of femur.....	.0197±.0021	.0279±.0025	— .0082±.0033
Tibio-tarsus.....	.0287±.0030	.0336±.0030	— .0049±.0042
Width of skull.....	.0128±.0013	.0245±.0022	- .0117±.0026
Keel of sternum.....	.0292±.0030	.0286±.0026	+ .0006±.0040

In all three series the individuals which survive are shorter than those which perish. The probable errors support in a very satisfactory manner the conclusion, "that when nature selects, through the agency of winter storms of this particular kind of severity, those sparrows which are short stand a better chance of surviving." For weight the results for the three series are also consistent in sign, and even when taken individually indicate

with a considerable degree of probability that the heavier birds are the least able to withstand the vicissitudes of the February sleet and snow. In all three series the length of the humerus is longer in the birds which survive, and in the group of adult males the difference is perhaps statistically significant. The same is true for the length of the femur, but the results are again insignificant except in the adult males where they are perhaps statistically trustworthy. In the adult males and in the adult and young females the length of the tibio-tarsus seems to be longer in the survivors, but the result is insignificant for the young males.

If selective elimination be a reality in nature one would not expect all of the characters of a series of individuals which perished when exposed to a given set of unfavorable conditions to differ from the same characters in the individuals which survive, and this for the simple reason that variations in many characters may not be of vital importance to the individual—in short, not of selective value.

The constants seem to me to justify no conclusion concerning the length of the sternum. For alar extent all three differences individually considered are insignificant; taken comparatively two are negative and one positive in sign. Apparently variations in the spread of wing have under the particular conditions[4] no significance in determining the chances of survival. The young males which survived have longer skulls (tip of beak to the occiput) than those which perished, and the difference seems to be significant in comparison with its probable error, but in the other two classes of birds the differences are not merely statistically insignificant but negative in sign.

Tables IV–VI show the standard deviations and their probable error. These are essential in calculating the probable errors of the means and in testing the hypothesis of a reduction in variability by selective elimination. Bumpus has discussed this question in detail in his lecture, but to me it seems that the standard deviations as given here do not justify any final conclusions concerning the relation of selection to variability: the problem is too complicated and the data are too few. As in other evolutionary problems we need more measurements. When these are available

[4] "Were the eliminative agent, for example, a severe northerly wind of protracted duration, the alar extent might then enter in as a factor of considerable selective value."

not only type and variability but correlation[5] will be open for investigation.

Looking at the tables of constants, the cautious biometrician will hesitate to say that Professor Bumpus has *proved* his point. The data available are too scanty to justify dogmatic assertions. But the work is so suggestive and the results so convincing that it is difficult to understand why zoologists have not followed it up by other studies of a comparable nature. To be sure, opportunities of this particular kind do not occur every winter, but there are other sources of elimination active in nature, and one of the most important tasks before those interested in the problems which Darwin pointed out to biologists, is to determine whether the individuals which survive are able to do so because of certain structural peculiarities, while those which perish are eliminated because they are in the degree of development or in the correlation of their parts structurally unfit.

J. ARTHUR HARRIS.

[5] Compare besides Bumpus's suggestion on this point, the arguments of Brooks in his "Foundations of Zoology," Lectures VI–VIII, and the hypothesis of Crampton, in *Journ. Exp. Zool.*, 2: 425–430, 1905.

NOTES AND LITERATURE

BIOMETRICS

An Introduction to Statistical Methods

In spite of the great development of biometric work, and of the application of statistical conceptions and methods in a number of fields of science other than biological, during the last decade there has been produced up to the present time no fully satisfactory introduction to the elementary principles of modern statistical methods. The books which have appeared in this field have been, broadly speaking, either (*a*) too technical and advanced in their treatment, or (*b*) compilations of formulæ with so little in the way of guiding principles as actually to lead any but the already expert into many difficulties, or (*c*) incomplete, incorrect and superficial at vital points, or finally, (*d*) have appealed to a very limited class of readers by developing the subject in direct relation to a narrow field of science only. This need for a comprehensive, elementary and sound introduction to statistical methods is admirably met in a recently published book by Yule.[1]

The subject is treated under three main heads as follows: (I) The Theory of Attributes, (II) The Theory of Variables, (III) The Theory of Sampling. In the first part the author deals with the logical basis of statistical theory, a field which is essential to a proper understanding of the subject, and in which he is, by the extent and character of his original investigations, qualified to speak with unique authority. Successive chapters in this portion of the work deal with Notation and Terminology, Consistence, Association, Partial Association, Manifold Classification.

The second part of the book takes up the discussion of frequency distributions and their physical constants, and the elementary theory of correlation and its applications, ending with an account of multiple and partial correlation. Here we are dealing with matters of immediate practical importance in the application of statistical methods to all kinds of scientific problems. It would be difficult to say too much in commendation of the author's method of treating these subjects. No knowledge

[1] Yule, G. Udny, "An Introduction to the Theory of Statistics," London (Chas. Griffin & Co.), 1911, pp. xiii + 376.

of mathematics beyond algebra up to the binomial theorem is presumed, yet the subject is developed in such a simple, lucid and at the same time thorough way as to give the reader a real and adequate grasp not only of the technique of the methods, but also of their origin and significance. Numerical examples drawn from a wide range of materials are given at every stage and worked out in detail. Particular attention is paid to guiding the unwary beginner around the numerous pitfalls which beset the statistical pathway. Chapters are devoted to the methods of arranging data in the form of frequency distributions, determining centering constants (arithmetic, geometric and harmonic means, mode, median, etc.), variation or "dispersion" measuring constants, and coefficients of correlation. The treatment of correlation is particularly comprehensive and practical.

The last section of the book deals with the general subject of "probable errors." The theory of fluctuations in statistical measures due to random sampling is developed first in relation to the theory of attributes and then in relation to the more complex theory of variables. The discussion of the simple sampling of attributes leads up in a straightforward way through the point binomial to the normal curve of errors, and the normal correlation surface.

Each chapter throughout the book is followed by a short list of selected titles of original papers, and a series of practical problems to be worked out by the student. Appendices give short bibliographies of calculating tables, tables of functions, etc., and general works on the mathematical theory of statistics and the theory of probability. A list of answers and hints in regard to the problems and a full index complete the volume.

Altogether the book is a notable one. Those who are familiar with Yule's paper "On the Theory of Correlation" (published in the *Journal of the Royal Statistical Society* in 1897) which has become one of the classics of biometric literature will be prepared to welcome the present work. It is marked throughout by the same clearness, directness and appreciation of the difficulties of the beginner which distinguished that memoir. For the non-mathematical student desirous of obtaining a sound working knowledge of the elements of modern statistical theory this book will be of the greatest value. In the field which it covers it is without a peer.

RAYMOND PEARL.

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Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

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THE
AMERICAN NATURALIST

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INHERITANCE OF FECUNDITY IN THE DOMESTIC FOWL[1]

DR. RAYMOND PEARL

MAINE AGRICULTURAL EXPERIMENT STATION

THERE are under discussion at the present time two general views regarding certain fundamental points in heredity. Each of these points of view has its zealous adherents. On the one hand, is what may be designated the "statistical" concept of inheritance, and on the other hand, the concept of genotypes. By the "statistical" concept of inheritance is meant that point of view which assumes, either by direct assertion or by implication, that all variations are of equal hereditary significance and consequently may be treated *statistically* as a homogeneous mass, provided only that they conform to purely statistical canons of homogeneity. This assumption of equal hereditary significance for all variations is tacitly made in deducing the law of ancestral inheritance, when individuals are lumped together in a gross correlation table.[2] The genotype concept, on the other hand, takes as a fundamental postulate, firmly grounded on the basis of breeding experience, that two

[1] Papers from the Biological Laboratory of the Maine Experiment Station, No. 25. This paper was read at the meeting of the American Society of Naturalists at Ithaca, December, 1910.

[2] For a more detailed discussion of this point see a paper by the present writer entitled "Biometric Ideas and Methods in Biology: their Significance and Limitations," in the *Revista di Scienza* (in press).

sorts of variations can be distinguished, namely those (*a*) that are represented in the germinal material and are inherited without substantial modification, as in "pure lines," and those (*b*) that are somatic and are not inherited. By anything short of the actual breeding test it is quite impossible to tell whether a particular variation observed in the soma belongs to the one category or to the other. As I have tried to emphasize in other places, it is both to be expected on this view of inheritance, and is also the case in actual fact, that the somatic manifestation or condition of any character is a most uncertain and unreliable criterion of the behavior of that character in breeding. Finally under the genotype concept, of course, the whole array of facts brought out by Mendelian experiments find their place.

Now while certain adumbrations of the genotype concept have long been current in biological speculations in regard to heredity, this general view-point owes its grounding in solid facts primarily to Johannsen's work with beans and with barley. It is to be noted that in these cases, as well as in most of the investigations of the pure line theory which have followed Johannsen's work, the organisms used have been such as reproduced either by self-fertilization, or by fission, or by some vegetative process. This brings us to the consideration of a question of great importance, both theoretical and practical. In cases of diœcious organisms, where a "*pure*" pedigree line in the sense that such lines are found in beans or in Paramecium by definition can not exist, has the genotype concept any bearing or significance? In a general way it obviously has. Probably no one (except possibly some of the ultra-statistical school) could be found who would deny that in general a distinction is to be made between variations having a gametic and those having merely a somatic basis. But specifically how far has the genotype concept any application in case of "non-selfed" organisms? Johannsen in his "Elemente" has thoroughly analyzed Galton's material and

shown that it is capable of a satisfactory and reasonable interpretation on the genotype hypothesis, and East and Shull have gone far in the analysis of genotypes in maize. This, however, is only a beginning. There is the greatest need for careful, thorough investigations of the inheritance of characters showing marked fluctuating variation in organisms having the sexes separate. Here lies one of the crucial fields in the study of inheritance to-day. Through the brilliant results in Mendelian directions and from the study of really "*pure*" lines we are getting clear-cut ideas as to the inheritance of qualitatively differentiated characters, such as color, pattern and the like, on the one hand, and in regard to the inheritance of quantitative variation in self-fertilized or non-sexually reproducing organisms, on the other hand. But beyond all these lie the difficult cases where in diœcious forms quantitative variations must be dealt with. If these can be cleared up and brought harmoniously into a general scheme or view-point regarding inheritance, we shall have gone a long way in the solution of this world-old biological problem.

For some four years past the writer has been engaged in a study of the inheritance of fecundity in the domestic fowl. The problem presented here is an important one from the practical as well as the theoretical standpoint. If definite and sure methods of improving the average egg production of poultry by breeding can be discovered it will mean much to the farmers of the nation. At the same time egg production is a character in some ways well adapted to furnish definite and crucial data regarding inheritance. Variations in egg production are readily measured, and can be directly expressed in figures.

The general results of this study of the inheritance of fecundity may be said, in a word, to be, so far as they go, in entire accord with the genotype concept, and not to agree at all with the "statistico-ancestral" theory of inheritance. Indeed, so ill is the accord here that the chief exponent of the latter doctrine has recently attempted to

throw the whole case out of court[3] by asserting that fecundity is not inherited in fowls, and that the present writer's investigations show essentially nothing more than that. It will be the purpose of this paper to present some figures sufficient to indicate with some degree of probability, I think, first that egg production in fowls *is* inherited, and second that it is probably inherited in accord with the genotype concept, in spite of the fact that we do not and can not here have "pure lines" in the strict sense of Johannsen's definition. In the present paper, owing to limitations of space, the whole of the data in hand obviously can not be presented. Only a few illustrative cases can be given here.

Before entering upon the discussion of the evidence it is necessary to call attention to two points. The first is in regard to the unit of measuring egg production used in the work. For reasons which have been discussed in detail elsewhere[4] the unit of study has been taken as the egg production of the bird before March 1 of her pullet year. This "winter production" is a better unit for the study of the inheritance of fecundity than any other which can be used practically. All records of production given in this paper are then to be understood as "winter" records, comprising all eggs laid up to March 1 of the first year of a bird's life. It may be said that the "normal" mean winter production of Barred Plymouth Rocks (the breed used in this work) is fairly indicated by the 8-year average of the Maine Station flock. This average November 1 to March 1 production is *36.12* eggs.[5] This figure is based on eight years continuous trap-nesting of the flock with which the present

[3] Pearson, K., "Darwinism, Biometry and some Recent Biology, I," *Biometrika*, Vol. 7, pp. 368–385, 1910.

[4] Bull. Me. Agr. Exp. Sta., No. 165. U. S. Dept. Agr. Bur. Anim. Ind., Bul. 110, Part II.

[5] It should be said that up to and including the winter of 1907 only the November 1 to March 1 records are available as a "winter" record. Since that time the small number of eggs laid before November 1 (on the average two or three per bird) are included in the "winter" totals. These, then, give, as stated, the total production up to March 1.

work was done, carried out before these investigations were begun.

In the second place it is desirable to call attention to some of the difficulties which attend an attempt to analyze the inheritance of the character egg production. The most important of these is the fact that this character is not visibly or somatically expressed in the male. A male bird may carry the genes of high fecundity, but the only way to tell whether or not this is so is to breed and rear daughters from him. All Mendelian workers will agree that it is sometimes difficult enough to unravel gametic complexities in the case of characters expressed somatically. It is vastly more difficult when only one sex visibly bears the character. In the second place a very considerable practical difficulty arises from the fact that egg production is influenced markedly by a whole series of environmental circumstances. The greatest of care is always necessary, if one is to get reliable results, to insure that all birds shall be kept under uniform and good conditions. Further, on this account, it is necessary to deal with relatively large numbers of birds. Some of the important conditions to be observed in work on fecundity have been discussed elsewhere[6] and need not be repeated here.

Turning now to the results we may consider first

The Effect of Selection for Fecundity in the General Population

On the "statistico-ancestral" view of inheritance it would be expected that if fecundity were inherited at all this character would respond to continued selection. That is, it would be expected, if the highest layers only were bred from in each generation, that the general flock average would steadily, if perhaps slowly, increase and that any level reached would be at least maintained by continued selection. In 1898 an experiment in selecting for high egg production was begun at the Maine sta-

[6] Me. Agr. Exp. Sta. Ann. Rept. for 1910, p. 100.

tion. In this experiment only such females were used as breeders as had laid over 150 eggs in their pullet year (corresponding roughly to an average winter production of 45 or more eggs) and the only males used were such as were out of birds laying 200 or more eggs in the year. This experiment was continued until the end of 1908. The selection, be it understood, was based on the egg record alone, and no account was kept of pedigrees or of genotypes. Every female with a record higher than 150 eggs in the year was used as a breeder regardless of whether her high fecundity was genotypic or phænotypic.

The results of this selection experiment covering a period of nine years have been fully reported elsewhere.[7] Here it needs only to be said that the net outcome of the experiment was to show that there was no *steady* or *fixed* improvement in average flock production after the long period of selection. There was no *permanently* cumulative effect of the eight (in the last year) generations of selected ancestry. So far from there having been an increase there was actually a decline in mean egg production concurrent with the selection, taking the period as a whole. During parts of the selection period, however, as for example the years 1899–1900 to 1901–02, inclusive, and the years 1902–03 to 1905–06, inclusive, an improvement from year to year was to be noted, but in each case the flock dropped back in intervening years. This is an important point, the meaning of which is now clear. The flock average from year to year depended largely upon *whether the breeders of the year before had had their high fecundity genetically represented or only somatically*. In some years the selection was fortunate in getting nearly all the breeders from good (*i. e.*, "high production") genotypes or from good *combinations* of genes. In other years just the opposite thing happened: the high layers chosen as breeders came from low geno-

[7] U. S. Dept. Agr. Bur. Anim. Ind., Bul. 110, Parts I and II, 1909 and 1911. *Zeitschr. f. indukt. Abst. a. Vererb.-Lehre,* Bd. 2, 1909, pp. 257–275.

types or combinations of genes. The general upshot was that while the selection of *high layers* merely as such was systematic year after year the result attained in the general flock production was entirely haphazard and uncertain. This is exactly what would be expected on the genotype hypothesis, but not on the "statistico-ancestral."

TABLE I

MEAN WINTER (NOVEMBER 1 TO MARCH 1) EGG PRODUCTION DURING THE SELECTION EXPERIMENT

Year	Mean Winter Production
1899–1900	41.03
1900–01	37.88
1901–02	45.23
1902–03	26.01
1903–04	26.55
1904–05	35.04
1905–06	40.66
1906–07	21.44
1907–08	15.92

The actual course of the average winter egg production (not hitherto published) during the period is given by the figures of Table I and shown graphically in Fig. 1.

Certainly the first line of evidence, derived from a long-continued experiment, involving more than 2,000 individuals, gives no support to the "statistico-ances-

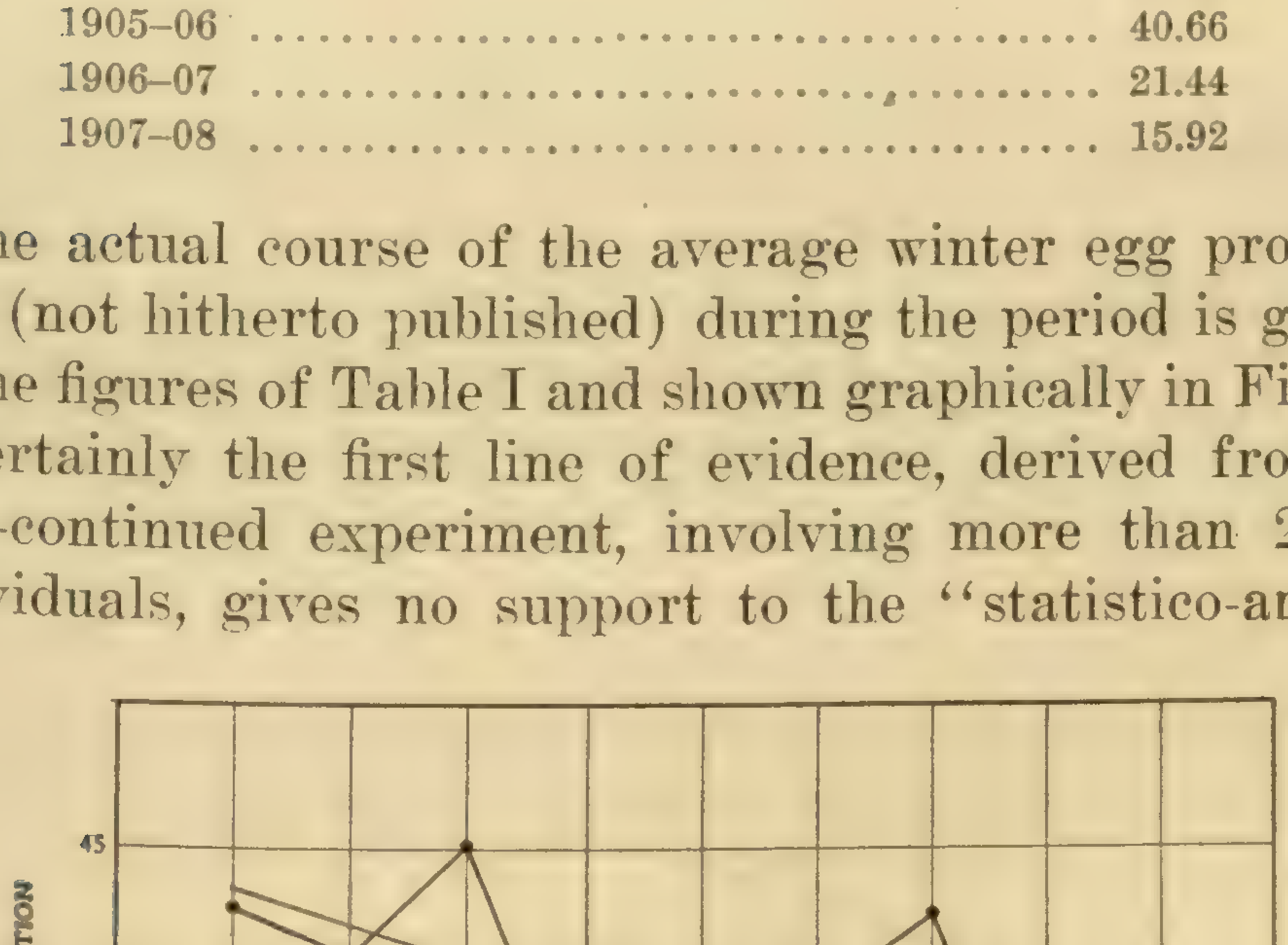

FIG. 1. Diagram showing the course of average winter egg production during the period covered by the mass selection experiment.

tral'' theory and indeed is in flat contradiction to one of the most fundamental tenets of that faith.

Let us next consider the question,

ARE SOMATICALLY EQUAL VARIATIONS IN FECUNDITY OF EQUAL HEREDITARY SIGNIFICANCE?

In the spring and summer of 1907 were reared 250 pullets, all of which were the daughters of hens that had laid approximately 200 or more eggs in the first year of their life. This group of mothers was reasonably homogeneous in respect to records of egg production. All had laid about the same number of eggs. Their daughters were, however, far from a homogeneous lot with respect to egg production.[8] It is plain from the results obtained in that experiment that the egg record of a hen is a most unreliable criterion of the probable number of eggs which her daughters will lay. This is demonstrated by examination of individual cases. Thus consider the two mothers nos. 253 and 14. Their winter production records were nearly identical (65 and 66 eggs, respectively). Their daughters' average winter productions were 23.87 and 2.40 eggs, respectively! Certainly it seems reasonable to conclude that the gametic constitutions involved in the breeding of 253 and 14 were quite different, though both these hens laid the same number of eggs. Again, take birds no. 386 and 911. One had a winter record of 55 and the other of 52 eggs. Yet their daughters' average winter productions were, respectively, 4.88 and 27.33 eggs. Many more instances of this kind could be brought forward. Taken together, the whole evidence shows beyond the shadow of a doubt that the presence of high fecundity in an individual, and that factor which makes high fecundity appear in the progeny, are two very different things, either of which may be present in an individual without the other. We plainly have here the basis for the distinction of phænotypes and genotypes just as in beans.

[8] Full details regarding this experiment have been published as Bull. 166, Me. Agr. Exp. Sta., 1909. See particularly Table I.

The Inheritance of Egg Production in Pedigree Lines

Let us now consider some of the evidence that such things as genotypes of fecundity really exist in fowls. We may first examine some representative pedigrees covering four generations and showing the occurrence of high and low fecundity lines.

As a typical example of a high fecundity pedigree line in which the high fecundity is genotypic, line D5D39 may be considered. In the presentation of this and other pedigree tables the following conventions are adopted. The band numbers of the birds are in bold-faced type, and following the band number of each female, her winter egg record is given in italic figures enclosed in parenthesis. The band numbers of males are given in italics.

Pedigree Line D5D39

♀ **D39** *(62)* × ♂ *D5*
- ♀ **E232** *(69)* × ♂ *555—0*
- **237** *(55)* × ♂ *554*

Mean = 62

136 *(48)*
- ♀ G **10** *(100)*
- **14** *(99)*
- **88** *(23)*
- **524** *(16)*

♀ **F255** *(48)* × ♂ *564*

303 *(64)* × ♂ *563*
- ♀ G **12** *(16)*
- **19** *(70)*
- **39** *(100)*
- **53** *(44)*
- **81** *(34)*
- **85** *(73)*
- **192** *(57)*
- **213** *(29)*

347 *(69)* × ♂ *562*
- ♀ G **18** *(61)*
- **27** *(83)*
- **46** *(116)*
- **196** *(56)*
- **211** *(36)*
- **248** *(67)*

363 *(74)* × ♂ *567*
- ♀ G **11** *(47)*
- **134** *(111)*
- **165** *(35)*
- **198** *(39)*
- **506** *(16)*

Mean = 61

Mean = 57.74

This line is shown graphically in Fig. 2.

Little comment on this pedigree line is necessary. We see a certain high degree of fecundity faithfully reproduced generation after generation. Different males were

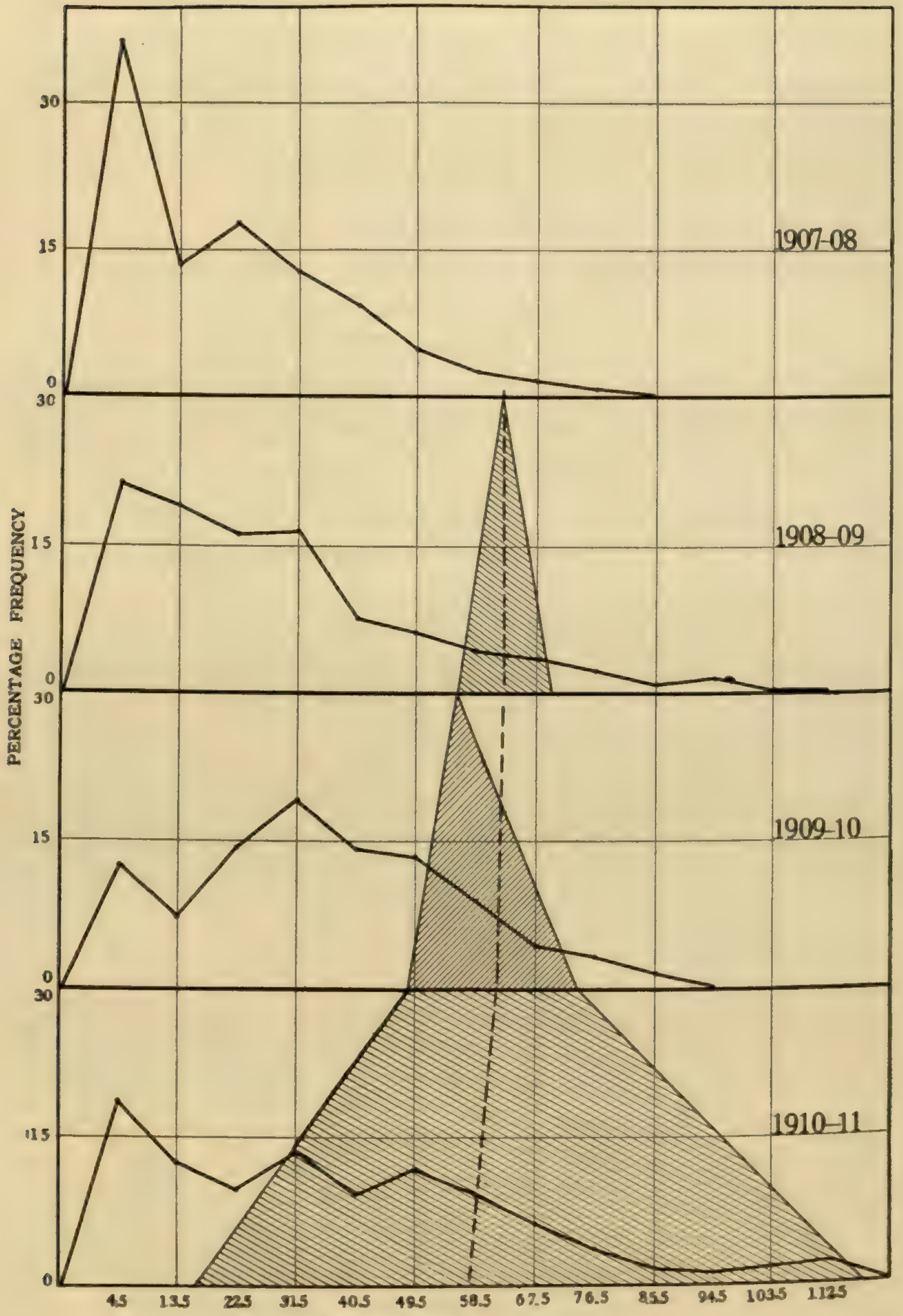

FIG. 2. Diagram showing range of variation and mean fecundity in each generation of line D5D39. The main polygons of variation give the distribution of fecundity in the general flock in each generation. The cross-hatched areas represent the pedigree line, and the heavy dotted lines through these areas represent the mean fecundity of the line in each generation.

used with different females, but in every case the males used were from high fecundity lines and were believed to carry this quality in their germ cells either in homozygote or heterozygote condition.

In marked contrast to the last example let us consider the *low* fecundity line D61D168. It is a troublesome matter to propagate the low fecundity lines, because of the difficulty of getting a sufficient number of eggs during the early part of the breeding season. The line D61D168 is of interest not alone as an illustration of a typical low line, but also because there appeared in it a mutation, or something very like one. We will consider here only the main line and not the mutant.

PEDIGREE LINE D61D168

♀ **D168**(*33*) × ♂ *D61*

- ♀ **E231**(*25*) × ♂ *552*
- **419** (*9*) × ♂ *551*
- **209**(*38*) × ♂ *555* — 0
- **313**(*26*) × ♂ *554*
- **363**(*11*) × ♂ *550*
- **15**(*18*)
- **163** (*9*)
- **200**(*12*)
- **141** (*0*)
- **116**(*28*)
- **151**(*11*)
- **24**(*23*)

Mean = *17.5*

- ♀ **F233**(*32*) × ♂ *573* — 0
- ♀ **F165** (*7*) × ♂ *569*
  - ♀ **G221**(*16*)
  - **430**(*12*)
  - **477** (*1*)

  Mean = *9.67*
- ♀ **F250**(*20*)
- **174**(*21*)
- ♀ **F249**(*30*)

Mean = *22*

♀ **E248**(*48*)[9]

This line is shown graphically in Fig. 4, in which the mutant and its progeny are also shown.

A low line in which no mutant has appeared, but in which also the mean production is not so low as in line D61D168 is D65D366. Since the egg production has not been so low in the early part of the breeding season with this line it has been easier to propagate it.

[9] This was the mutant referred to. Its progeny will be considered later. See p. 335.

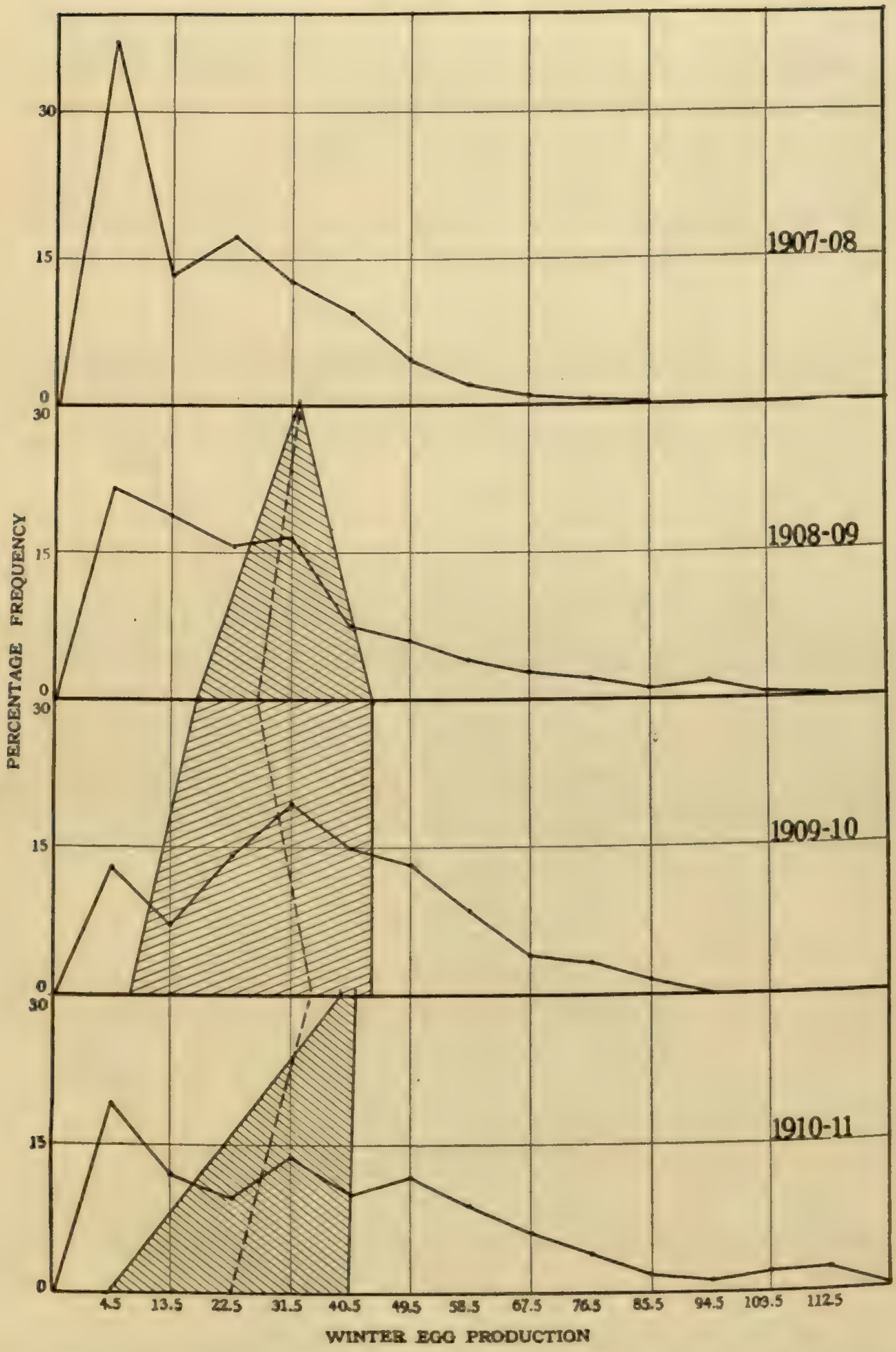

FIG. 3. Diagram showing range of variation and mean fecundity in each generation of line D65D366. Significance of lines and cross hatching as in Fig. 2, *q.v.*

PEDIGREE LINE D65D366

♀ **E239**(*24*)×♂*553*	♀ **F309** (*OD*)[10]			
	263(*44*)			
	362(*43*)		♀ **G 34** (*4*)	
	216(*41*)×♂*569*		**42** (*37*)	
			56 (*40*)	
			164 (*5*)	
	224(*43*)×♂*554*	♀ **F301** (*7*)		
		223(*14*)		
		224(*42*)		
♀ **D366**(*33*)×♂*D65*			♀ **G 65** (*28*)	
	354(*15*)×♂*551*	♀ **F242**(*21*)	**209** (*33*)	
		221(*39*)×♂*566*	**267** (*25*)	
			502 (*21*)	
			544 (*8*)	
	331(*31*)×♂*552—0*			
	344(*17*) ×♂*550*	♀ **F271**(*37*)		
	344(*17*) ×♂*528*	♀ **F171**(*46*)		
	Mean=26	*Mean=33.4*	*Mean=22.33*	

This line is shown graphically in Fig. 3.

In the examples thus far given we have had to do with pedigree lines in which a given degree of fecundity reappeared from generation to generation with practically no change. In two instances quite certainly, and possibly in several others, a new and distinct variation has suddenly appeared within a line and thereafter bred true, thus presenting the characteristic phenomena of mutation. The most striking instance of this sort occurred in line D61D168 and may be given here in detail. The main part of this line has already been discussed (p. 331). It will be recalled that it is a line of low fecundity. In 1908 there appeared in it one individual of distinctly higher fecundity than any other bird in the large family of that year. This individual when bred produced only high layers. In the next generation two of these daughters were bred to males known to belong to high fecundity genotypes (♂♂554 and 566). One of these matings unfortunately produced no adult female offspring. The other led to the production of six adult daughters, all of which are relatively high layers, with the single exception of G495, which has a record of only one egg, and that record is doubtful. This bird has probably never laid an egg, and almost certainly is pathological.

[10] Bird died during winter period.

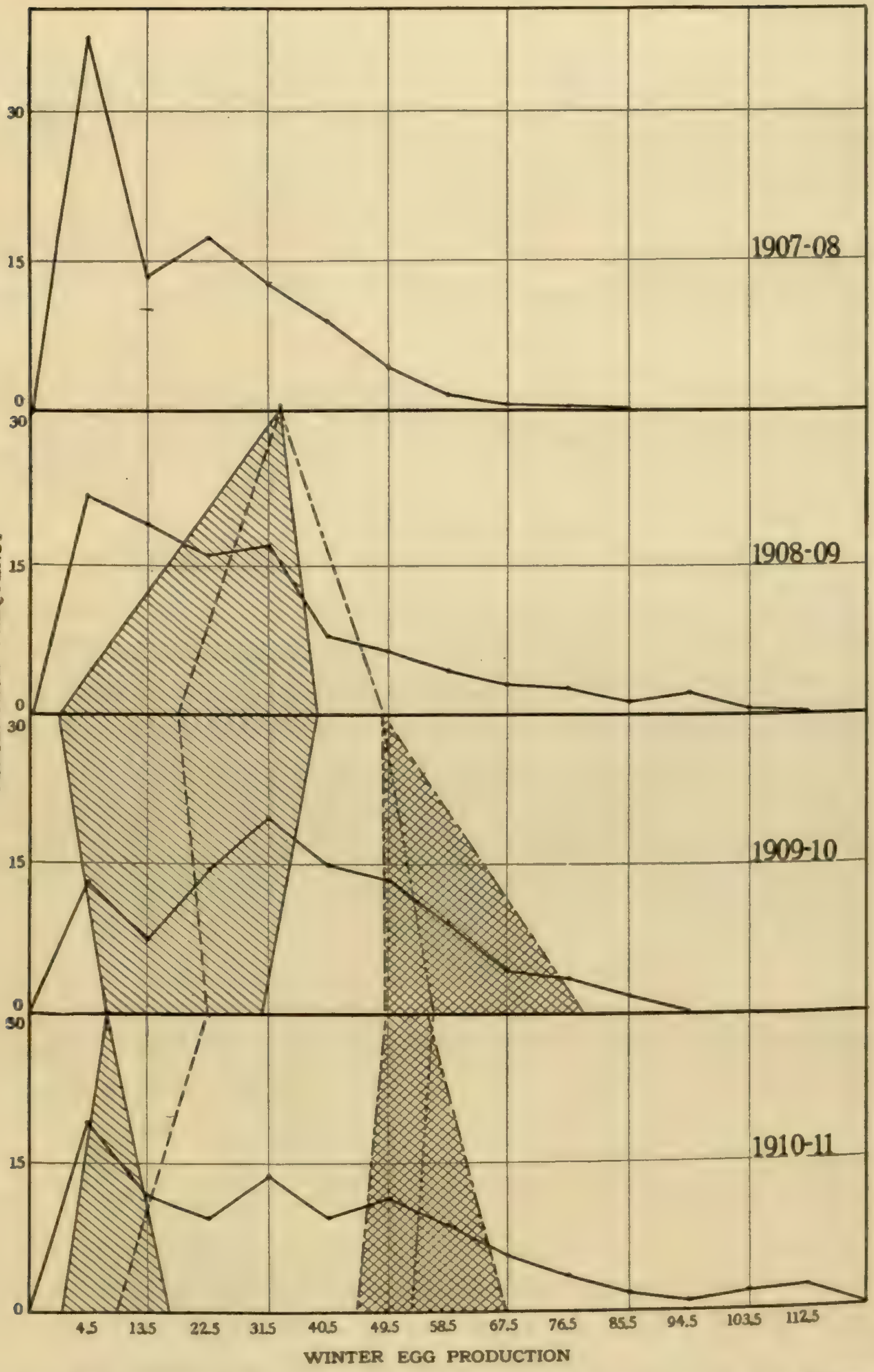

FIG. 4. Diagram of pedigree line D61D168. The significance of lines is the same as in Figs. 2 and 3, except that the mutant line is double cross hatched. For the sake of simplicity E495 and the daughters of D31 are omitted in the 1910–11 generation.

Leaving this bird out of account because pathological, the mean winter production of the family is 52.8 eggs, very strikingly different from the average (9.67 eggs) of the birds of the same generation in the main low line in which the mutation appeared.

Two other daughters of the mutant E248 were mated to ♂D31, a bird known not only to belong to a genotype of mediocre to low fecundity, but to be remarkably prepotent in respect to this character, so that practically regardless of the females with which he has been mated the get has been uniformly poor in respect to egg production. Four adult females resulted from the two matings under discussion. They have an average winter production of 23.75 eggs. There are several possible explanations of this result, but the most probable is that we have here simply one more instance of the extraordinary prepotency of ♂D31.

The last of the daughters of the mutant was mated to a cross-bred male, no. 578, and consequently the progeny can not fairly be compared with the pure Barred Rocks in respect to fecundity.

The facts here briefly discussed are shown in the following table and graphically in Fig. 4.

It is apparent from the table and the diagram that the main line and the "mutant" line are entirely distinct. Indeed they do not overlap in their ranges even excepting only the pathological individual G495. The "mutant" pullet E248, for some reason or other, possessed the capacity both to lay a relatively large number of eggs, and the genes necessary to make this quality appear in her progeny. Whether this individual is to be regarded as a true "mutation" would appear to be largely a question of definition. In the writer's opinion the most probable explanation is that E248 is a Mendelian segregation product. That is, let it be supposed that both D168 and D61 were heterozygous with respect to degree of fecundity, and were producing in some (unknown) ratio both "high fecundity" and "low fecun-

PEDIGREE LINE D61D168 (COMPLETE)

♀ **D168** (*33*) × ♂ *D61*

♀ **E248** (*48*) × ♂ *553*

♀ **F308** (*78*) × ♂ *554*—0

354 (*55*) × ♂ *566*

♀ **G 30** (*45*)
62 (*58*)
117 (*46*)
197 (*66*)
428 (*49*)
495 (*1*)

Mean of high line=52.8[11]

166 (*49*) × ♂ *D31*

♀ **G204** (*41*)
254 (*15*)

141 (*51*) × ♂ *D31*

♀ **G229** (*28*)
458 (*11*)

Mean of D31's daughters=23.75

172 (*50*) × ♂ *578—Cross*

Mean of mutant (high) line=56.5

♀ **E231** (*25*) × ♂ *552*

♀ **F233** (*32*) × ♂ *573*—0

419 (*9*) × ♂ *551*

♀ **F165** (*7*) × *569*

♀ **G221** (*16*)
430 (*12*)
477 (*1*)

Mean of main (low) line=9.67

209 (*38*) × ♂ *555*—0

313 (*26*) × ♂ *554*

♀ **F250** (*20*)
174 (*21*)

363 (*11*) × ♂ *550*

♀ **F249** (*30*)

Mean of main (low) line=22.0

15 (*18*)
163 (*19*)
200 (*12*)
141 (*0*)
116 (*28*)
151 (*11*)
24 (*23*)

Mean of main (low) line=17.5

dity'' gametes. Then E248 may be supposed to have originated from the union either of two ''high fecundity'' gametes or one high and one low fecundity gamete. She then would be either a DD or a DR bird, on the assumption, which the facts seem to support, and which I have more fully discussed elsewhere,[12] that high fecundity is dominant over low.

[11] Omitting G495. See text.

[12] ''Inheritance in 'Blood Lines' in Breeding Animals for Performance, with Special Reference to the '200-egg' Hen,'' Rept. Amer. Breeders' Assoc., Vol. VI, 1911 (in press).

The subsequent breeding history of E248 indicates that it was probably a DD bird, though the reasons for this opinion can not be fully gone into here. The general view, recently emphasized by Nilsson-Ehle,[13] that phenomena of mutation are, in many cases at least, merely cases of Mendelian segregation has much evidence in its favor.

The pedigrees which have been given are merely illustrations. Many other similar ones might be cited from the records in hand did space permit. In the experiments during the past three years the attempt has been made to propagate separately lines of high, medium and low fecundity. In the course of this work it has been found that lines of high fecundity were nearly if not quite as likely to have originated with individuals of a low record of production as with those of a high record. Similarly, many low fecundity lines have originated with individuals which were themselves exceedingly high layers. Indeed one of the highest winter layers which have ever appeared in the stock evidently belonged to a genotype of very low fecundity, since it has never been able to produce progeny of anything but the poorest laying capacity. The breeding history of this bird (D352) is indeed so interesting that it may be briefly discussed here. This bird in her pullet year laid 98 eggs between November 10 and March 1 and made a record for the year of over 200 eggs. She was mated and produced plenty of eggs during the hatching season, but they hatched very badly. Only one female worth putting in the house was obtained. This pullet (E356) made a winter record of only 39 eggs, just about the general flock average. E356 was not mated. Her mother (D352) was kept over and bred to another male the next year, in the hope that as a fowl she might produce more and better chickens than she had as a pullet. As a matter of fact she was again able to produce during the whole

[13] Nilsson-Ehle, H., "Kreuzungsuntersuchungen an Hafer und Weizen," *Lunds Univ. Arsskr.*, N. F., Afd. 2, Bd. 5, Nr. 2, 1909, pp. 1–122.

breeding season only one pullet worth putting into the laying house. This pullet (F163) made a winter record of but 11 eggs. F163 was bred in 1910, but produced only one daughter worth saving. This daughter, G429, has made a winter record of 18 eggs. It would be hard to get clearer evidence than that afforded by this breeding history that D352 belonged to a low fecundity genotype, in spite of her individual high laying record.

THE EFFECT OF THE SELECTION OF FECUNDITY GENOTYPES

Let us now consider the bearing of the results so far set forth on the problem of selection. Taking first the question of the effect of selection for fecundity within a population it is plain that if different degrees of fecundity have a genotypic basis, as the facts above presented and a considerable mass of data of a similar kind, which owing to lack of space can not be given here would appear to indicate, then the results following selection will depend entirely upon the genotypic constitution of the population. If high fecundity genotypes are present they can be isolated by selection. If they are not present selection of high laying hens will not change the average production of the flock.

The aim of the selection experiments since 1907 has been to discover and propagate separately genotypes of high fecundity and genotypes of low fecundity, all the birds being taken from the same general flock. The results of this work are shown in the following table and in Fig. 5. This table is to be regarded as a continuation of that given on p. 327, *supra*, which shows the results of mass selection for high fecundity in the same stock.

EFFECT OF SELECTION FOR FECUNDITY WITHIN THE POPULATION

1907–08.	Mean winter production of general population	15.92
1908–09.	Mean winter production of all high fecundity lines	54.16
1908–09.	Mean winter production of all low fecundity lines	22.06
1909–10.	Mean winter production of all high fecundity lines	47.57
1909–10.	Mean winter production of all low fecundity lines	25.05
1910–11.	Mean winter production of all high fecundity lines	50.58
1910–11.	Mean winter production of all low fecundity lines	17.00

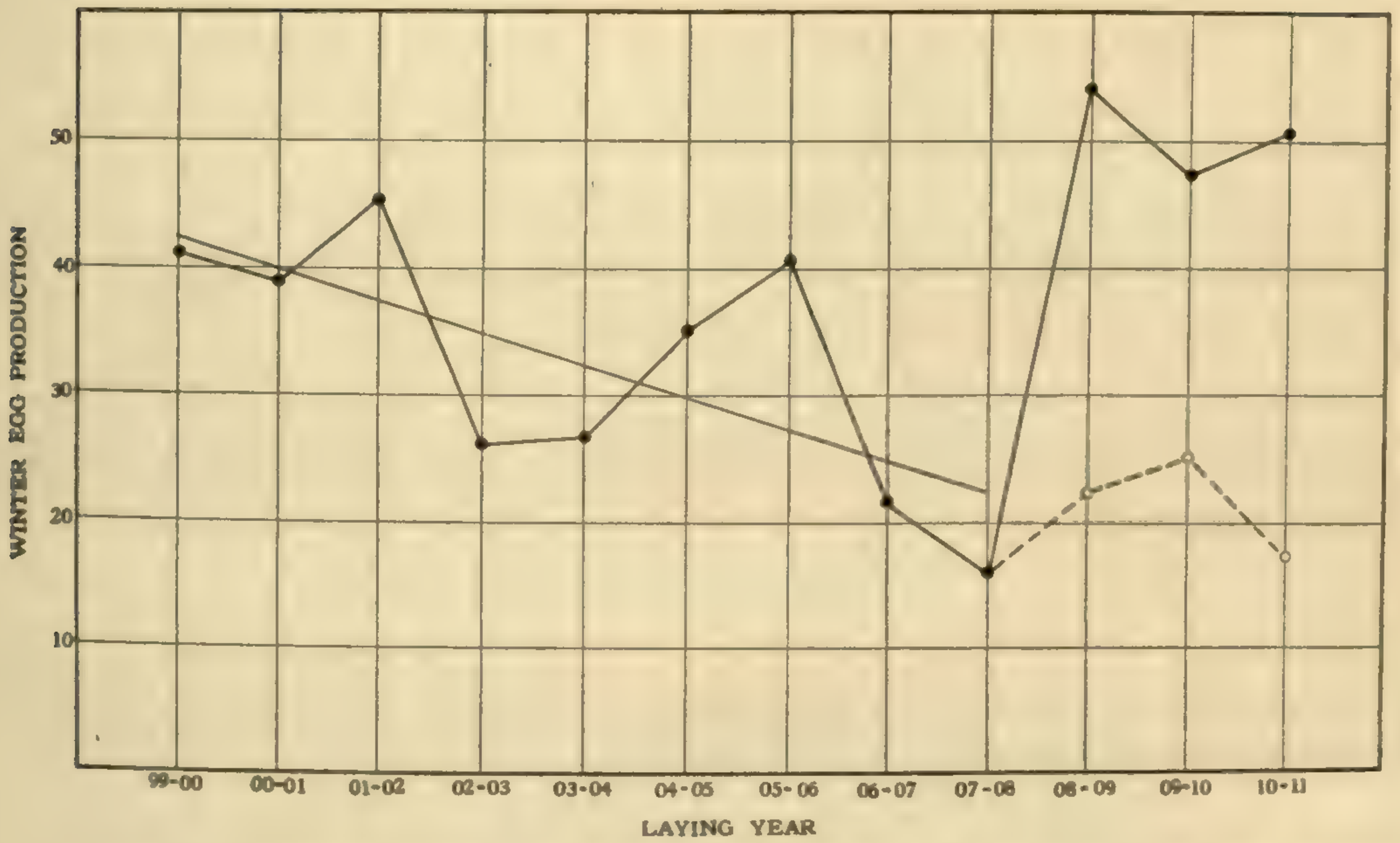

FIG. 5. Showing the effect of selecting high and low fecundity on a genotypic basis. The solid line denotes means of all "high lines"; the dotted line means of all "low lines." Up to 1907–08 the attempt had been to increase egg production by breeding merely from the highest layers, regardless of pedigrees. In 1907 and subsequent years the attempt has been to isolate genotypes of high and low fecundity which shall breed true, each to its own type.

The results indicate the effectiveness of this method of selection. It should be understood, of course, that only those pedigree lines are included in the high line averages which uniformly *in each generation* show high fecundity. A similar consideration applies to the low line averages.

Let us now consider briefly the question of the effectiveness of selection *within* the genotype. According to the "pure line" concept we should not expect selection of high or low individuals belonging to the same genotype to produce any effect, except in cases where segregation has occurred and the selected individuals are really gametically different, though having the same pedigree. An example of this sort has been given in the case of line D61D168 (cf. p. 331, *supra*). The ineffectiveness of selection within the line when something of this sort does not occur is illustrated by line D56D407. In the F_1 generation in this line there were four birds, of which three were good layers and one was a poor layer. Two of the good layers and the poor layer were bred.

Large families were reared in F_2 and F_3. The average results in the three generations are given in the following table.

EFFECT OF SELECTION OF GOOD AND POOR WINTER LAYERS IN THE SAME LINE, D56D407

Generation	F_1	F_2	F_3
Mean winter record of *good* layers and their progeny	76.0	46.7	35.57
Mean winter record of *poor* layers and their progeny	26.0	52.0	36.75[14]

It is evident that selection within the line here was quite without effect.

Another example of the same thing from line D31D447 may be given by way of further illustration. In this line there was in the F_1 generation a family of ten daughters. Of these some were very good and some were poor layers. All were bred. The mean results are shown in the next table.

EFFECT OF SELECTION OF GOOD AND POOR WINTER LAYERS IN THE SAME LINE, D31D447

Generation	F_1	F_2	F_3
Mean winter record of *good* layers and their progeny	62.5	23.75	22.00
Mean winter record of *poor* layers and their progeny	32.0	28.75	14.75

Here again it is plain that selection within the line was without effect. Many more examples of the same sort might be given from the records did space permit. In general there is no evidence whatever that the selection of individuals of different laying records, but belonging to the same fecundity genotype, produces any definite or permanent effect whatever.

DISCUSSION AND CONCLUSIONS

Taking into consideration all the facts which have come out of this study, one is led to the following view as to the composition of a flock of fowls in respect to fecundity. In the average flock we may presume that there will probably be represented a number of fecundity

[14] If one family of four birds, which ought not in fairness to be included here because they were extremely inbred (brother-sister mating) in connection with another experiment, is excluded this average becomes 49.0.

genotypes, some high, some low, and some intermediate or mediocre. In an ordinary flock these genotypes will be greatly mixed and intermingled. Further, the facts in hand indicate that the range of variation in fecundity *within* the genotype is relatively very large, nearly as great, in fact, as in the general population. Thus while fecundity genotype *means* may be and usually are perfectly distinct, there is much overlapping of individuals in the different lines. In consequence it results that the egg record of an individual bird is of almost no value in helping to tell in advance of the breeding test to what fecundity genotype it belongs. Essentially this same fact has been brought out in all of the work which has been done with pure lines. The only difference in the present case lies in the fact that the range and degree of variation within the line appears to be relatively greater in the case of fecundity than in the case of most characters hitherto studied, as, for example, size relations in beans or *Paramecium*.

The most serious difficulty which confronts one in the attempt to analyze the inheritance of a character like fecundity lies in the almost inextricable mingling of genotypes in the great majority of individuals. This, of course, is a direct consequence of the manner of reproduction. The germ plasm of two separate individuals must unite to form a new individual. By prolonging incestuous mating one may in theory come indefinitely close to reproductive purity, but in practise even this is extremely difficult, if not impossible of accomplishment on any large scale or through any long period of time. The fact simply is that a "pure line" in the strict sense of Johannsen[15] can not by definition exist in an organism reproducing as the domestic fowl does. This, however, by no means indicates that the inheritance of fecundity does not rest on a genotype basis, or, in other words, that

[15] Johannsen's definition is as follows: "Mit einer reinen Linie bezeichne ich Individuen, welche von einen einzelnen selbstbefruchtenden Individuum abstammen." ("Ueber Erblichkeit in Populationen und reinen Linien," p. 9.)

fowls do not carry definite genes for definite degrees of fecundity.

We touch here upon an important point; namely, the relation of the mode of reproduction to the mode of inheritance. As one reflects upon the matter it becomes clear that it is only in the sense of a *reproductive* line that we can not, by definition, have pure lines in organisms where the sexes are separate. It is perfectly possible to have a line of such organisms in which all the individuals are *gametically* pure with reference to any particular character. For example, it is the simplest of matters to establish a line of horses pure in respect to chestnut coat color. Any individual in such a line mated to any other will never produce anything but chestnut offspring. So similarly with any other character, it is only necessary to obtain homozygous individuals in respect to any character in order to form a gametically pure strain with reference to that character.

It must further be kept clearly in mind that a reproductive "pure line" (in the sense of Johannsen's definition) may be made up of individuals *not* gametically pure (*i. e.*, homozygous). Thus suppose one crosses a yellow and a green pea and then takes an F_2 heterozygote individual seed which originated from a self-fertilized F_1 individual as the "single, self-fertilized individual" with which to start a line. The individual which starts such a line arose by self-fertilization and is selfed to produce progeny and would thus fulfil every requirement of a *reproductive* "pure line" as defined by Johannsen. Yet it would produce both yellow and green offspring. On the other hand, as already pointed out, a line which is not, and from the nature of its mode of reproduction never can be, reproductively "pure" may be gametically so (*i. e.*, have none but homozygous individuals with respect to any character).

We then see that the fact that in fowls the sexes are separate and we therefore can not have reproductive "pure lines" gives, *per se*, no reason to suppose that fe-

cundity is not inherited on a genotypic basis. We have to consider the problem of genetic or gametic purity. Do we have homozygote lines in such cases as those discussed in this paper? It plainly is the fact that one can get lines of birds which, broadly speaking, will breed true (perhaps throwing occasionally a few individuals not true to the type of the line) to definite degrees of fecundity. The same thing is true of milk production in dairy cattle, speed in race horses, etc. What are these lines gametically? Theoretically the formation of gametically pure (homozygote) lines with respect to definite degrees of fecundity is simple. Practically it is exceedingly difficult to do this, owing to the fact that (*a*) the character studied is not expressed in the male, and (*b*) it is subject to a wide fluctuating variability caused by environmental conditions. The question as to the gametic constitution of the fecundity lines here discussed obviously can not be answered finally now. It is a matter for much further research. One may, however, form a general conception of the probable gametic constitution of such lines, which has much evidence in its support. The essential points in such a conception are:

1. Probably no line yet obtained is absolutely pure gametically in respect to fecundity. It represents a mixture of a greater or less number of fecundity genes.

2. Lines which breed reasonably true to a definite degree of fecundity may in most cases be taken to be made up of individuals bearing a preponderant number of genes of the particular degree of fecundity to which the line breeds true, so that in gametogenesis a great majority of the gametes formed carry only these genes. They also carry some genes of higher, or lower fecundity, or both kinds. When individuals of a definite (*e. g.*, "high") line thus constituted are bred together the majority of the offspring will, purely as a matter of chance, be produced by the union of two high fecundity gametes. It is quite possible that with families of the size obtained with poultry nearly or quite every individual produced

in the line for several successive generations may be of this kind. In the long run, however, it is to be expected that a small number of "off" individuals will appear in the line. These originate by the chance union of two low fecundity genes, or by the union of a "high" gene with a "low" gene of great potency (as in the case of D31, cf. p. 335).

3. The degree to which such a line will breed true will depend upon the proportion of genes of one type (or of very similar types) present. The higher such proportion the less frequently will the "off" individual segregate out. The practical goal to be worked towards is, of course, to obtain several lines not closely related, but all made up only of individuals homozygous with respect to either high or low or any other definite degree of fecundity.

Whether a given degree of fecundity is to be regarded as a single unit character, in the Mendelian sense, or, on the other hand, as a complex dependent upon a particular combination of separately segregable unit characters, can not yet be determined. Every one must recognize the fundamental importance of the investigations of Nilsson-Ehle, Baur and East, which have shown that many characters which at first glance do not appear to conform to any determinate law of inheritance are really complexes, formed by the combination of a number of unit characters, each of which segregates and otherwise behaves in a perfectly regular and lawful manner. There are some facts which indicate that high fecundity is a character of this kind, but it will require prolonged analysis to decide this, because of the numerous practical difficulties which attend the study of fecundity.

A great help in this analysis, as well as a contributory line of evidence of much weight in supporting the general conception of the manner of inheritance of fecundity set forth above, is derived from the study of crosses between breeds of poultry in which high and low degrees of fecundity are definite breed characters. Studies of

this sort carried out at the Maine station indicate that the relatively high fecundity characteristic of the Barred Rock breed is inherited as a sex-limited character. In this respect it behaves like a simple unit character, but this does not necessarily prove that it is not a complex. More data are needed to settle this point. Of much significance is the fact that, whether simple or complex, fecundity is shown by these experiments in cross breeding to be a character resting on a definite gametic basis.

In conclusion, I think it may fairly be said that the investigations here reported show in the first place that different degrees of fecundity *are* inherited in the domestic fowl, and in the second place, that in all respects wherein it has been possible, considering the inherent difficulties of the material and the character dealt with, to make the test, the method of this inheritance is in entire accord with Johannsen's concept of genotypes.

THE BIOMETRIC PROOF OF THE PURE LINE THEORY[1]

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I. INTRODUCTION

ON this platform I find myself in a somewhat embarrassing position. A friend assured me in advance that this symposium would be somewhat analogous to the country parson's "praise service," and into this pure devotional atmosphere I must bring a note of agnosticism.

Agnosticism is a term selected after careful deliberation. Johannsen's propositions are important—if true—and any candid naturalist must hesitate before opposing a new theory which may lead to important advances in biology. Agnosticism is the condition of mind temporarily enforced by the results of my own experiments. If one is pledged in advance to the pure line theory many of these observations can be made to confirm Johannsen's conclusions. If one is unprejudiced and seeks to fit his theories to his observations, rather than to adjust his facts to his preconceived conclusions, the results are quite as capable of other interpretation. Possibly more extensive work may show clear confirmation of his results. Meanwhile I must withhold final judgment, merely stating that my own work has greatly shaken my confidence in Johannsen's theory.

Here I do not care to dwell upon details of my own experiments. It seems more profitable to try and state the fundamental problems of the pure line theory as they appear to the biometrician and to indicate the methods of work which seem to him necessary to the drawing of sound conclusions.

[1] From a symposium on "The Study of Pure Lines of Genotypes," before the American Society of Naturalists, December 29, 1910.

II. The Fundamental Propositions of the Pure Line Theory

Our symposium has for its subject the Genotype or Pure Line Theory. Some of the speakers have enthusiastically urged us to replace the words "pure line theory" by "pure line facts." If this were done there would be little need for this program. Pure line facts are as yet a very insignificant part of biological data. The real occasion for this symposium is the pure line theory—the rank vines which have grown from the nineteen bean seeds which Johannsen planted in 1901. Biologists would have been little interested by the statement that selection within the offspring of a single bean has been ineffective in changing the weight of the seed. It is the daring generalization of the conclusions drawn from these limited experiments—the curt characterization of other researches as of no biological significance or their reinterpretation (from flounder's fins to intelligence in school children) in terms of the bean experiments, that forces us to take an interest in these matters.

Our first problem is to ascertain what these generalizations—the elements of the pure line theory as contrasted with the pure line facts—are. Our second task is to try to ascertain in how far experimental facts support the pure line theory.

Davenport[2] has given a particularly good outline of Johannsen's theory:

> The fundamental principle of Johannsen is that an ordinary frequency polygon is usually made up of measurements of a characteristic belonging to a non-homogenous mass of individuals; that it is really analyzable into several elementary masses each of which has a "frequency polygon" of its own. In each elementary polygon the variation is strictly due to non-inheritable somatic modifications, selection of extremes of which has no genetic significance. But the selection for breeding of individuals belonging to different elementary polygons, lying, say, at the extremes of the complex, may quickly lead to an isolation of these elementary polygons, the constituent individuals of which reproduce their peculiarities as distinct elementary species.

[2] Davenport, C. B., *Science*, n. s., 30: 852, 1909.

We recognize three essential propositions:

Proposition 1.—Most species or varieties are not homogeneous, but are composed of a large number of minor forms.

The series of individuals classified as the same variety or race by the systematist, regarded as homogeneous material for experiment by the physiologist, lumped together to form a single "population" by the statistician, is designated by Johannsen as a phænotype. This phænotype may generally be analyzed by pure line breeding into many constant and indivisible strains known as genotypes.

Systematists have long regarded certain groups as polymorphic. *Aster*, *Rubus*, *Salix* and *Cratægus* at once occur to the botanist and *Unio*, *Salmo* and the staphylinids to the zoologist. But the genotype theory seems to regard systematic polymorphism as a much wider phenomenon. Indeed one is sometimes assured that every apparently uniform cultivated variety is a swarm of constant biotypes. Johannsen emphasizes the generality of heterogeneity. For instance, he says:[3]

> Ein gegebener Phaenotypus mag Ausdruck einer biologischen Einheit sein; es braucht es aber durchaus nicht zu sein. Die in der Natur durch variationsstatistische Untersuchungen gefundenden Phaenotypen sind es wohl in den allemeisten Fällen nicht![4]

Again on page 162:

> In der Praxis wirkt ein Selektion meistens schnell in der beabsichtigen Richtung—eben weil die Bestände oder Populationen fast immer Gemische sind.

One more illustration will suffice:

> Der oft ausserordentlich grosse Reichtum genotypischer Unterschiede in einer auscheinend einheitlichen Population war von Darwin . . . ebensowenig in der vollen Tragweite erkannt, als es dem grossen Grundleger der Mikrobiologie, Pasteur, klar sein konnte, welche bedeutung es hatte,

[3] "Elemente," p. 123.

[4] On page 121, he remarks on this point: "Selbst die shönste 'typische' Verteilung beweist gar nichts in Bezug auf Einheitlichkeit des derart in Erscheinung tretenden Typus." Professor Johannsen is apparently unaware that this point has been fully recognized by "Biometriker" for years.

dass viele physiologisch sehr differierende Heferassen in vermeintlich 'reinen' Hefekulturen koexistieren konnten.[5]

Proposition 2.—These genotypes are separated generally by differences which are exceedingly minute.

Notwithstanding the constant flood of new species segregated from the classic Linnean groups, necessitating frequent supplements to "Index Kewensis" and other works of its kind, many naturalists could hardly understand the small species discussed by de Vries in his great work. Indeed, many laboratory men hardly perceived the usefulness of recognizing species—perfectly constant, we were assured—so closely related that one taxonomist could not identify the species of another from his descriptions; species so similar that herbarium material was worthless, and only culture side by side could distinguish them. Yet after a lapse of only ten years we find de Vries criticized for not recognizing even smaller divisions than these! Spillman says: "de Vries overlooks entirely those closely related pure lines, differing frequently only quantitatively, and in a single character. . . . They not only do not differ in all their characters as the *Œnothera* mutants do, but their norms present a regular series coming under Quetelet's law."[6]

As examples of these minute differences both he and Lang[7] quote the "72 Formen einer Population einer gewissen Heferasse" discussed by Nilsson-Ehle.[8]

Jennings says:[9]

> The work with genotypes brings out as never before the minuteness of the hereditary differences that separate the various lines. These differences are the smallest that can possibly be detected by refined measurements taken in connection with statistical treatment. Johannsen found his genotypes of beans differing constantly merely by weights of two or three hundredths of a gram in the average weight of the seed. Genotypes of *Paramecium* I found to show constant hereditary differences of one two-hundredths of a millimeter in length. Hanel

[5] "Elemente," p. 318.
[6] Spillman, W. J., Am. Nat., 44: 760, 1910.
[7] Lang, A., *Arch. f. Induktive Abstamm.- u. Vererlungsl.*, 4: 15–16, 1910.
[8] Nilsson-Ehle, H., *Bot. Not.*, 1907: 113–140.
[9] Jennings, H., Amer. Nat., 44: 144–145, 1910.

found the genotypes of *Hydra* to differ in the average number of tentacles merely by the fraction of a tentacle. That even smaller hereditary differences are not described is certainly due only to the impossibility of more accurate measurements; the observed differences go straight down to the limits set by the probable errors of our measures.

Proposition 3.—These genotypes are rigid hereditary units; by a process of mutation one may give rise to another, but selection within the genotype is incapable of effecting a change.

This theory is everywhere so prominent in the writings of the genotypists that discussion or explanation is superfluous.

III. THE CARDINAL PROPOSITION OF THE GENOTYPE THEORY

Of these three essential propositions of the genotype theory of heredity, the first two might be accepted by Darwinian or Lamarckian or by a member of almost any school. If the proposition concerning the exceeding smallness of the differences be true, the theory might seem to present the greatest difficulty to the de Vriesian,[10] for with smaller and smaller genotypes there is a constant approach to continuity, but we are assured that continuity is never realized.[11]

The third proposition—that genotypic differences are rigid and unchangeable except by mutation—is therefore the essential one. The most obvious way in which this hypothesis can be tested against concrete facts is to determine the effect of selection upon genotypes.

The very heart of the pure line theory is the proposi-

[10] Jennings (AMER. NAT., 44: 145, 1910) tells us, "The genotype work lends no support to the idea that evolution occurs in large steps, for it reveals a continuous series of the minutest differences between great numbers of existing races."

[11] Johannsen ("Elemente," p. 356) says in criticism of the Lamarckian theory: "Die Lamarckismus muss kontinuierlich verschiebbare Typen annehmen; wir finden aber bei genauer Prüfung immer und immer wieder Diskontinuität."

tion that selection within the pure line is ineffective.[12] The strenuousness with which this has been maintained has even engendered in some minds the opinion that selection has no rôle at all to play in evolution or in practical breeding. The attitude of many appears to be that Darwin was quite mistaken when he wrote, "The key is man's power of accumulative selection: nature gives successive variations; man adds them up in certain directions useful to him."

Darwin said, "If selection consisted merely in separating some very distinct variety, and breeding from it, the principle would be so obvious as hardly to be worth notice." Fifty years after this was written we hold a symposium to celebrate the discovery that selection is after all merely the isolation of distinct varieties!

Was Darwin right or wrong? Have all practical breeders except those at the oft-quoted Svalöf station been chiefly occupied in wasting their time for the last fifty years? These are very important questions.

The burden of proof obviously lies on the genotypists.[13] Much of the evidence offered is most general and not at all *unzweideutig*. Indeed, when closely analyzed much of the reasoning reduces to a circle of three arcs each of one hundred and twenty degrees:

1. *Definition.*—A genotype or biotype is an organic unit, reproducing itself constantly[14] except for the transitory, non-inheritable modifications due to environmental influence.[15] It is not capable of change by selection.

[12] Johannsen ("Elemente," p. 137) states the problem: "Wird Selektion von Plus—oder Minus—Varianten innerhalb reiner Linien eine Typenverschiebung bezw. eine Galton'sche Regression hervorrufen?"

[13] To be acceptable, the evidence must be quantitative; the observations must either be numerous enough that variations due to uncontrollable factors will average out, or the experiments be conducted with such refined technique that environmental influences are entirely excluded; the statistical reasoning concerning the observations must be logically sound.

[14] "A biotype is a group of individuals which do not differ from one another in any hereditary quality and which therefore constitute a pure race."—Shull, G. H., *Am. Breed. Mag.*, 1: 100, 1910.

[15] "In a given 'pure line' (progeny of a single individual) all detectable

2. *Observation.*—Selection has never been known to produce a change in a genotype. Whenever, as is often the case, selection does result in modification of type this proves that the material considered was impure—that more than one genotype was originally present—or that others arose by mutation, and entirely irrespective of selection.

3. *Conclusion.*—It is therefore proved that selection can not modify the characters of a genotype.

Johannsen has written a very thick and a very convincing-looking book, but if one pins himself down to the task of going from cover to cover he finds that an unfortunate amount of the evidence reduces to this kind of reasoning—in short, to no critical evidence at all.[16] But behind this citing of examples which are not inconsistent with his theory although they prove nothing concerning it; besides this reiteration of testimony which merely excites in the minds of the court-room spectators suspicions concerning the integrity of the defendant without entitling the plaintiff to a verdict before an impartial jury,[17] there are certain direct experimental studies

variations are due to growth and environmental action, and are not inherited.''—Jennings, *Proc. Am. Phil. Soc.*, 47: 521, 1908.

''The standard deviation and coefficient of variation express in a pure race mere temporary conditions of no consequence in heredity. If we could make all conditions of growth and environment the same throughout our pure race, all the evidence indicates that the standard deviation and coefficient of variation would be zero, and this is the positive value of their assistance in determining what shall be the characteristics of the progeny.'' —Jennings, AMER. NAT., 43: 333, 1909.

''Wenn es gelänge, für alle Individuen einer reinen Linie absolut gleiche Lebenslage zu schaffen, müsste die Standardabweichung gleich sein.''—Römer, T., *Arch. Rassen- u. Gesells.-Biologie*, 7: 437–438, 1910.

[16] For instance, he (''Elemente,'' p. 162) refers to the fact that Hallet was unable to improve Le Couteur's wheat, although he had succeeded in improving seventy other samples from all parts of the world, and explains it by the assumption that in every case the seventy series of wheat were mixtures of biotypes while Le Couteur's was a pure line. This may be true, but what is it worth as scientific evidence?

[17] In working over the literature of the pure line theory the lover of fair play is sometimes on the verge of losing his patience, for although the experimental data—at least those which are confided to his reader—upon which Johannsen grounds his own theory are very slender, he is unsparing

which have been adduced in support of the genotype theory. These arguments and the evidence upon which they rest must be examined. For convenience of treatment I do this under three propositions concerning selection, which seem so reasonable that I believe few biologists will feel inclined to deny their soundness. They are at least so reasonable that no worker can afford to leave them out of consideration.

A. Characters which are not Inherited at all can not be Taken to Prove that Selection in General is Ineffective

This is a point of great importance, generally ignored by pure-linists. Biometricians have long known that of the variations of any character whatever not all are inherited.[18] They have also learned that variations in certain characters are not inherited.

Suppose now that one takes a character which gives no correlation between its degree of development in

in his criticism of the pioneer studies which have made his own work possible. Such bald statements as (''Elemente,'' p. 285), ''Alle solche Schlüsse sind aber für die eigentliche Erblichkeitsforschung gänzlich ohne Wert,'' seem to have little of profit to contribute to science. Johannsen's *ipse dixit* has been taken as gospel. Woltereck (*Verh. Deutch. Zool. Ges.*, 1909: 115) says, ''Dieses Resultat erschüttert ernstlich die grundlagen der statistischen Variations; und Erblichkeitforschung, wie sie von die Galton-Pearsonschen Schule betrieben wird.'' A. Lang (*Verh. Deutch. Zool. Ges.*, 1909: 24) asserts, ''Die biometrischen Forschung arbeitet mit unreinen material.'' Römer (*Archiv f. Rossen- u. Ges.-Biol.*, 7: 427, 1910) tells us, ''Variabilitätstudien sind bis in die neueste Zeit meist an Material ausgeführt worden, dessen Einheitlichkeit jeweils als sicher angenommen wurde, das aber nach dem jetzigen Stande der Wissenschaft als unrein angesehen werden muss. Dies tritt besonders hervor bei den veilen Untersuchungen der Biometriker.''

[18] This is one of the facts which has led the biometrician to discuss probabilities while biologists in general clamor for certainty in the individual instance. One of the results of recent experimental work that has been hailed with the greatest enthusiasm is that two individuals may be identical in external appearance and yet produce entirely different offspring: in short, that some (somatic) variations are and some are not inherited. The experimental data collected on this point both by pure line and by Mendelian researches are of high value, but those who hail them as novel simply parade their ignorance of much of the pioneer work in variation and inheritance.

parent and offspring in a population and selects to increase or decrease it. He will get no result of selection. If now he takes the same character and selects from the plus and minus variations within a pure line, he will again effect no change by selection. Does either of these cases prove that selection in general is ineffective? Or does the second support in any way Johannsen's genotype theory of heredity? Certainly not.

Certain important work of Pearl and Surface seems to me to deserve mention in this connection.[19] These researches are sometimes referred to as furnishing evidence against the possibility of improvement by selection, and this they do so far as the character with which they have dealt is concerned. In the generalization of their results, however, the greatest caution must be used.

From two series of experiments with the same strain of Barred Plymouth Rock fowls they show that there is little hope of increasing the egg-laying capacity by direct selection for fecundity. These results are doubtless of much practical importance. Biologically they are of interest in confirming the results of other biometric studies which have shown that for man, horse, swine and mice fertility is very slightly inherited in the population. To consider them as indicating that selection in general is ineffective would be a very grave error, for fertility—so far as we may judge from the statistics so far published—seems to be a character *sui generis* in respect to inheritance. To cite these results in support of Johannsen's genotype theory of heredity, as has sometimes been done, is absurd.

Is it not possible that Johannsen's results with beans may be due to seed weight being a character which is not inheritable at all in the population, and which can not, therefore, reasonably be expected to be inherited within the pure line?

[19] Pearl, R., and F. M. Surface, "Inheritance of Fecundity," Bull. Me. Ag. Exp. Sta., 166, 1909. Pearl, R., and F. M. Surface, "Is there a Cumulative Effect of Selection?" *Zeitschr. Ind. Abstamm.- u. Verebungsl.*, 2: 257–275, 1909.

Biologists will agree, I believe, that to test critically the effectiveness of selection in the population and in the pure line, the experimental material must be an apparently homogeneous wild species or a garden variety the individuals of which are not differentiated into subraces by characters other than those under consideration.[20] Conclusions drawn from any experiments in which these simple precautions are neglected seem of doubtful value.

From Professor Johannsen's first memoir, that of 1903, we have no reason to suspect that his material is not, so far as the biologist can judge, homogeneous.[21] We are told nothing of any vegetative differences seen during the two generations grown in 1901 and 1902. Apparently all the numerous reviewers have considered his material perfectly homogeneous except for differentiation into genotypes with respect to seed characters.

In his book, however, one notes with some surprise the casual information ("Elemente," p. 311) that his Pure Line I also has curiously bent seeds, a special "Verhalten" in germination and a "groben Habilus" in the vegetative organs. Indeed Johannsen states that from the form and method of germination, etc., of a seed—even though a strong "minus Abweicher"—he can generally recognize an individual belonging to Line I.

These points should have been made clear at the beginning. If Professor Johannsen's lines really differ in their vegetative characters, so, for instance, that they can be distinguished as they grow in the field, it seems to me that their significance for the efficiency of selection is

[20] Surely we can all agree that the population is to be an apparently homogeneous one, *i. e.*, such that all the individuals would be classified together by a keen taxonomist. If this is not the case, if by definition, "population" means to the pure linist a mixture of several conspicuously different things, there seems little need for further discussion.

[21] Of the seed he says, "Der Ausgangspunkt dieser Untersuchungen war eine gekaufte Partie, etwa 8kg, brauner 'Prinzessbohnen,' wohl eine der altesten Kruppbohnen unten den vielen Kulturformen von *Phaseolus vulgaris*. Die betreffende Ware . . . war ausgezeichnet schön und so gleichmässig, wie es überhaupt hier erwartet werden konnte."

greatly reduced. We do not know to what extent the differences in seed weight which give the low correlation in his population are due to the mixture of races slightly differentiated with respect to their vegetative characters. If this differentiation be considerable, the seed weight character with which Professor Johannsen has chiefly worked, may not be inherited at all in the population providing this population be one composed of individuals with the same vegetative characters. It is not sufficient to be assured that these classic beans differ "nur (oder fast nur)" in seed characters; more detailed information is much needed, and until it is forthcoming I must differ from most biologists in my opinion as to the importance to be attached to the conclusions drawn from them.

B. Improvement for any Single Character can not be supposed to be Unlimited

This is a fundamental consideration too often neglected.[22] A wheat is selected up to its maximum productiveness, perhaps by getting the uppermost attainable limit at one choice from a large field. Then because it can not be made to yield all grain and no stubble we are told that selection can only isolate already existing types. A sugar beet can not be all sugar and the cow can not give pure cream.

In arguing for Johannsen's theory East[23] concludes that since Illinois is no longer making progress in high

[22] The principle, however, has been clearly seen by some biologists. For instance, in his "Foundations of Zoology," Brooks says (p. 165): "A breeder of domesticated animals or of cultivated plants, who devotes his attention to one or two characteristics, must soon reach a point where no further improvement is practicable unless the species is at the same time greatly modified in many other respects." And again (pp. 177–178), "No one can dispute the well-known fact that this sort of *pedigree selection* for a single point quickly grows less and less effective, and soon reaches a maximum; but this is no proof of any 'principle of organic stability,' or anything else except the truth that long ages of natural selection have made the organism such a unit or coordinated whole that no great and continuous change in one feature is possible unless it be accompanied by general or constitutional change."

[23] East, E. M., "The Rôle of Selection in Plant Breeding," *Pop. Sci. Mo.*, 77: 198–199, 1910.

and low oil and protein selection in maize, their work has been merely the isolation of pure and constant strains—"sub-races"—with the characteristics in question as strongly developed in the beginning as we now find them, but continually intercrossing. The case is too complicated for discussion in detail, but certainly the fact that the characters can no longer be increased by selection[24] is no strong argument for the biotype idea. Under its present morphological and physiological organization we have no reason to suppose that the corn grain can be made to contain as much oil as the castor bean.

Again Pearl and Surface[25] announce concerning their selection work with corn,

> We find the results of this experiment or investigation to be very difficult (if not altogether incapable) of rational explanation in accordance with the biological implications of the "law of ancestral inheritance" and conclude that the results agree better with the genotype theory of Johannsen than with that of the cumulative theory of selection with, of course, the limitations implied by the fact that it is an open fertilized plant.

What Pearl and Surface have actually done is to take a desirable sweet corn which they for convenience designate as Type I, and attempt—with initial success—to improve it for yield in ears and stover, for configuration of ears, and especially for earliness. But this Type I corn is descended from a few ears, the offspring of which have been grown in Maine for fifteen to twenty-five years. The variety originally introduced must have been an

[24] That changes due to selection are at first rapid and then slower has long been recognized. Indeed, as early as 1869 Hallett stated as two of his laws of the action of selection, "The improvement which is at first rapid, gradually, after a long series of years, is diminished in amount, and eventually so far arrested that, practically speaking, a limit to the improvement in the desired quality is reached. By still continuing to select the improvement is maintained and practically a fixed type is the result."

Darwin's views on this question are partly expressed in a letter of 1869 to Sir Joseph Hooker ("More Letters," 1: 314), "I am not at all surprised that Hallett has found some varieties of wheat could not be improved in certain desirable qualities as quickly as at first. All experience shows this with animals."

[25] Pearl, R., and F. M. Surface, "Experiments in Breeding Sweet Corn," Me. Ag. Exp. Sta. Bull., 1910.

early one as compared with sweet corn in general, to be able to survive at all in Maine. During the fifteen to twenty-five years the ancestors of the Type I corn were grown in Maine it must have been[26] subjected to an occasional natural selection, for seed could be taken by the farmers from only plants which had ripened their ears. The somatic organization of some plants is such that they require only a few hours for their life cycle, but so long as sweet corn has the general characteristics of root, shoot and leaf that identify it as *Zea Mays* it seems reasonable to suppose that there is some limit to the reduction of the time required for germination, growth and fruiting—an irreducible minimum beyond which selection can not carry it. Surely the fact that Pearl and Surface could not continually reduce the time required for growth while at the same time maintaining a selection for yield of ears and stover may indicate that the irreducible minimum for earliness has been reached in a variety of the physical type they wish to breed. Speaking for myself alone, I must say that the data before us prove nothing against the theory of cumulative effect of selection, and they certainly do not furnish any critical evidence for the Johannsenian theory.

It seems to me that Pearl and Surface again tacitly make this unjustifiable assumption that the modification attainable for any single character is practically unlimited when they consider that their failure to increase egg production by selection is a legitimate argument against the potency of selection. Indeed they say of "200 egg hens," which lay an egg fifty-five per cent. of the days of the year, "This figure is of some interest as indicating what a *relatively* small proportion of the theoretically maximum character is being selected to, when 200-egg birds are bred."[27]

But why, pray, is two hundred and sixty-five and a quarter eggs per year the *theoretical maximum?* One

[26] Judging from the account of the difficulties of growing sweet corn which the authors give us.

[27] Pearl and Surface, Bull. Me. Ag. Exp. Sta., 166: 55.

ignorant of the physiology of reproduction in the domestic fowl might innocently suppose that even a hen needs a rest. If this be true, may it not be that 200 eggs is about the attainable maximum (the physical or physiological limit of the organism) of this variety under the environmental conditions available and that the Maine strain of poultry will not do better than it has? If this is not the attainable limit, why not assume over an egg a day as the theoretical maximum?

C. Selection can not in general carry a Character beyond a Degree Consistent with the Optimum for Maintenance and Reproduction

This proposition is perhaps in a sense explanatory of the one immediately preceding. A characteristic is not independent of, but correlated with the other characteristics of the organism, and if it increases or decreases unduly they must also change or the organism be made more or less unfit for survival.

Have those who claim to have found selection ineffective been selecting against the morphological or physiological balance of the organism, that is in a manner to render the organism less capable of maintenance, growth and reproduction?

If this be true their failure to obtain results will be in some measure explained.

A possible illustration of this case may be furnished by the work of Pearl and Surface on egg production in the domestic fowl. Their work is again chosen not because of any malicious desire to differ from them[28] in interpretation, but because in a brief discussion of the evidence for the genotype theory one must confine his attention to the most important of Johannsen's supporters.

The data are: (*a*) The results of an eight years' selec-

[28] The criticism presented here must not be interpreted as drawing into question the scientific value of the data or the practical importance of the results of the studies criticized, or be extended to other work of the same authors, but is to be limited to the question of interpretation in relation to the pure line problem.

tion for high egg production; (*b*) a correlation between the egg production of thirty-one individual mothers and the egg production of their daughters, and the comparison of the egg production of these daughters with that of a large number of pullets of unregistered female parents.

We note the following details:

1. During the eight-year selection experiment[29] some unfavorable environmental accidents occurred in certain of the laying years. The averages for these years are perhaps too low, and both the actual means and a series of corrected means are given. The corrected means show an insignificant increase, but the unmodified means show a pronounced decrease in mean number of eggs as the result of the eight year selection.

2. In correlating between the egg production of the 31 highly selected mothers and their 217 daughters there is not trustworthy evidence of any relationship between the fertility of the mothers and that of their daughters.[30] *If these constants show any deviation from 0 whatever it is on the negative side.*

3. In comparing the daughters of these "200-egg" hens with three other series of the same strain but not of such highly selected female parentage, both for winter and spring egg production, it is shown that in five cases out of six the offspring of less highly selected parentage are better layers than those of the less stringently selected parents.

Thus all three comparisons indicate that the high laying mothers tend to produce low laying daughters; selection to increase egg production actually decreases it.

[29] "The practise in breeding was to use as mothers of the stock bred in any year only hens which laid between November 1 of the year in which they were hatched and November 1 of the following year, 160 or more eggs. After the first year, all male birds used in the breeding were the sons of mothers whose production in their first laying year was 200 eggs or more. Since the normal average annual egg production of these birds may be taken to be about 125 eggs, it will be seen that the selection practised was fairly stringent." *Zeit. Ind. Abst.- u. Verebungsl.*, 2: 261, 1909.

[30] From a knowledge of the biometric work of the last several years this is just the result which one would have expected to get.

Such a run of results as this can hardly be due to chance.[31] They indicate rather the presence of some as yet undetermined physiological factor.[32]

Candidly viewed and considered in comparison with other biometric work on the inheritance of fertility and fecundity, I think these experiments can not be held to be strongly opposed to the theory of the effectiveness of selection in general. However this may be, they certainly afford no substantiation for Johannsen's genotype theory of heredity.

IV. Summary and Conclusions

By the genotype theory of Johannsen one understands the following propositions:

An apparently uniform population or phænotype is generally not homogeneous, but is composed of a large number of differentiated types, which are to be designated—within limitations to be laid down immediately—as genotypes.

Externally, the genotype can not be distinguished from the phænotype. Both may have normal variation curves, but while that of the phænotype may by proper selection be broken up into constituent genotypes, the variation curve of the genotype can not be modified by selection. In short, the genotype is from the standpoint of heredity a rigid unit. All individuals belonging to the same genotype have the same potencies as parents. Only discontinuous segregations or transformations—mutations—may modify them.

[31] The argument that this observed decrease as the result of selection to increase egg production is due to chance must rest chiefly on one or both of two assumptions. First, that the eight-year selection experiment is absolutely untrustworthy because of the accidents which may have affected the egg production in certain years adversely. Second, that 31 mothers is a number entirely too small to give significant results in the case of a character like fecundity. These admissions would vitiate entirely any conclusion concerning selection to be drawn from these experiments.

[32] To me it seems that some of Pearl and Surface's published data are most suggestive of the nature of this factor, but they doubtless have in progress experiments that will throw light on these matters and biologists will await their results with interest.

The keystone of the pure line arch is the proposition that selection is ineffective except as a means of separating already existing genotypes. If this keystone-proposition be not sound the whole structure of the theory crumbles.

The propositions of the genotype theory are such that scientific proof or disproof is rendered particularly difficult. By theory selection can not effect a change in a pure line; by a slippery process of reasoning in a circle any results attained by selection are at once discredited by the assertion that the original material was impure. If, on the contrary, any selection experiment is ineffectual it is by some process of reasoning quite incomprehensible to some of us, at once chalked up to the credit of the new theory. If heritable differences appear within a pure line known to be so, these results are also discredited by the assertion that the observed change is a mutation or has been produced by the action of the environment. Truly the unbiased investigator is between the devil and the deep sea!

The actual experimental data upon which the genotype theory rests are as yet few. Johannsen's conclusions for beans depend chiefly upon the offspring of only nineteen seeds, and so far as I am aware no other investigator has confirmed his results on *Phaseolus*. Hanel had only twenty-six original *Hydra*, and Pearson's analysis of his data with more adequate methods than he used, evidences against rather than for the genotype theory. Jennings gives us the records of only six selection experiments involving altogether only a few actually selected *Paramecia*. Considering the large environmental and growth factors, his conclusions can not be considered as beyond question.[33] The work of Pearl and Surface with poultry and maize seems to me to have

[33] In offering this criticism I wish to express the highest admiration for Professor Jennings's two memoirs on variation, heredity and evolution in the protozoa. The coupling of refined statistical with careful experimental methods in the investigation of these organisms marks a great advance in biology.

no critical bearing on the pure line problem.[34] This is also true of numbers of other smaller experiments which can not be cited.

If one turns from the strictly pure line side of the problem to the more general questions of the "something" or "Etwas" in the germ plasm which determines in large degree the somatic characters of the individual which develops from it, one can only suggest that nothing whatever is explained by giving another name to a well-known fact. Ever since the time of Darwin, and before, we have known that there was "something" in the germ cells which determined the character of the offspring. We have had a dozen different names for this something, and by adding a thirteenth, "Gene," Johannsen has merely burdened us with another cloak for our ignorance. Unfortunately biological closets are full of such cloaks, once in fashion—now out.

Finally, I must make my own position quite clear. With Professor Jennings's contention that pure line cultures are of fundamental importance in many fields of physiology and genetics, I am in hearty agreement. Like other breeds of facts, "pure line facts" can not become too abundant. Indeed, *a priori,* I am not opposed to the genotype theory. As a theory it is most attractive, but one can not accept it without proof on that account. Personally, I am one of "that last small remnant" who believe that in a problem of this kind the proof must be biometric. This means merely three things. In so far as the nature of the material permits, all the data considered must be quantitative. The data must be numerous enough that biological relationships will not be obscured by the errors of random sampling. The data must be analyzed by logically sound methods.

Judged by these standards, I must express the conviction that as yet there is no adequate justification for the genotype or pure line theory.

[34] Naturally, this is purely a matter of interpretation, and does not diminish in the slightest degree the value of the work.

THE INFLUENCE OF CHANGED EXTERNAL CONDITIONS ON THE DEVELOPMENT OF TWO SPECIES OF MOTHS

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THESE experiments were carried out in the fall and winter of 1908–09, and their results are not without interest even though no marked changes in the insects were effected.

I. *Attacus cecropia* LINN.

Cocoons of this large Saturniid were collected in New Jersey in December and January. The controls, kept in their cocoons, were hung out-of-doors exposed to rain and sun until the latter part of April, then placed in a hatching cage in a room at out-of-doors temperature, when they hatched in May. The pupæ to be experimented upon were removed from the cocoons and kept in horizontal positions unless otherwise specified.

A. *Experiments with Light*

Direct Sunlight.—Four pupæ, lot no. 86, of which only one was healthy in appearance, were placed in direct sunlight in a warm room (21° C.) on February 5; one of them hatched on February 10 and laid eggs, while the other died. Evidently direct sunlight is not fatal to them.

Direct Sunlight behind a Heat Filter.—Twenty pupæ, lot no. 83, were laid horizontally on their dorsal surfaces with heads directed towards the sunlight, behind a vertical flat glass jar containing a saturated aqueous solution of alum, in a warm room (21° C.). They were thus placed on January 22, and all hatched in March following.

Diffuse Sunlight.—Five pupæ, lot no. 65, were placed, each vertical with head up in a test-tube in a room that never sank quite as low as freezing; all hatched between May 15 and June 2.

Five pupæ, lot no. 66, were kept under similar conditions, but placed with their heads down in the test-tubes; four of these hatched in May, the fifth being infected by parasites. Three pupæ, lot no. 69, were placed vertically in separate tubes within a moist chamber near a steam radiator in my private laboratory; two hatched in February, the third died.

B. *Experiments with the Tracheal Stigmata Covered*

Twenty pupæ, lot no. 85, were placed in a warm room (21° C.) in diffuse sunlight. On January 22 the stigmata, of which there are eight easily recognizable pairs counting those of the head, were covered with a gum-arabic solution, but this peeled off and was replaced the next day by pure Canada balsam. It is, however, quite doubtful how efficient the balsam was in excluding air from the respiratory tubules, for it does not adhere very well to the greasy surface of the cuticula. Four of these pupæ, lot 85A, had seven stigmata of the right side covered, and all hatched. Four others, lot 85B, had the first pair of stigmata covered, and all hatched. Four others, lot 85C, had the second and third pairs of stigmata covered, and all hatched. Four others, lot 85D, had the sixth and seventh pairs covered, and three hatched. Four others, lot 85E, had the fourth pair covered, and three hatched.

C. *Experiments with Higher Temperatures*

Ten pupæ, lot no. 68, were placed within a closed and dry glass jar in diffuse light, kept thus at 28° C. for 23 days, then removed from the jar and kept in diffuse light in a room at 21° C. All hatched, except three that were parasitized.

Twenty-two pupæ, lot no. 80, were placed on January

5 in an egg incubator at 39° C., kept there for varying periods, then removed into a warm room (diffuse light, 21° C.) until hatching. These were divided into lots as follows:

80A, 4 pupæ, incubator 1 day, all hatched in March.
80B, 3 pupæ, incubator 2 days, all hatched in February and March.
80C, 3 pupæ, incubator 3 days, 2 hatched in March.
80D, 3 pupæ, incubator 4 days, all hatched in March.
80E, 3 pupæ, incubator 6 days, 2 hatched in February.
80F, 3 pupæ, incubator 7 days, all hatched in February and March.
80G, 3 pupæ, incubator 28 days, all hatched in March.

Twelve pupæ, lot no. 84, were placed in an egg incubator from January 22 to February 18, then removed to diffuse light in a warm room (21° C.) for hatching; the temperature in the incubator was 39° C. until January 28, after that 39.5° C. Nine of these hatched in March and April.

D. *Experiments with Lower Temperature*

Seven pupæ, no. 41, were placed in a tight covered and dry glass jar in an ordinary ice refrigerator from December 7 to March 29, afterwards removed to a warm room; three hatched May 17, the others were destroyed by an accident.

Thirteen pupæ, no. 67, were treated similarly; two hatched on May 17, the others were killed accidentally.

E. *Results of the Experiments*

The pupæ were exposed to unusual external conditions: removed from the cocoon, exposed to direct sunlight with and without a heat filter, to diffuse light, to various temperatures ranging from 0° C. to 39° C., with the stigmata covered with balsam, in horizontal and vertical positions. Yet nearly as great a proportion hatched as in the case of the controls. Higher temperatures hastened the rate of development. Further, the pupæ so abnormally treated did not differ in coloration from the controls or to no extent that could be measured;

this result applies to the pattern as well as to the intensity of the coloration. For in the controls quite as great a range of color variation was found as in the others. Also the unusual conditions of life did not appear to effect the dimensions of the hatched moths. To decide this I took as the most convenient measurement the length of the fore wing, measured from its point of insertion against the thorax to the most anterior edge of a dark spot placed anteriorly near the apex of the wing; I did not measure to the extreme free edge of this wing, for that portion is very flexible and liable to become folded during the process of mounting the moths. The right wing was measured unless it happened to be misshapen. Only about a hundred moths were preserved, too few for any statistical study of this wing length, consequently in the following table only the extremes of variation of this length are given (expressed in millimeters, and accurate to within a half millimeter).

Lot 40	(1♂, 5♀)	control	♂ length 67.5	♀ length 69.0–74.5
Lot 64	(2♂, 6♀)	control	♂ length 61.0–65.0	♀ length 61.0–75.5
Lot 68	(4♂, 3♀)		♂ length 58.0–64.0	♀ length 64.0–73.0
Lot 69	(2♂)		♂ length 66.0–67.0	
Lot 79	(3♂, 3♀)	control	♂ length 59.5–65.0	♀ length 69.0–75.0
Lot 80	(7♂, 7♀)		♂ length 61.5–70.0	♀ length 61.0–73.0
Lot 82	(3♂, 6♀)	control	♂ length 67.0–69.0	♀ length 66.5–74.0
Lot 83	(12♂, 6♀)		♂ length 60.0–68.5	♀ length 67.0–73.0
Lot 84	(2♂, 4♀)		♂ length 67.0–67.5	♀ length 68.0–71.5
Lot 85	(12♂, 3♀)		♂ length 63.0–69.0	♀ length 65.5–73.0

It is probable that this late pupal stage is so advanced in its development that it can not become much modified by external changes.

II. *Thyridopteryx ephemeræformis* Steph.

This psychid is the common "bag-worm" or "basket-worm." The larva immediately on hatching constructs a bag or cocoon of silk covered with portions of leaves or chips, and increases the size of the bag as it grows and carries it about. At the end of the summer each attaches its bag firmly to the twig of a tree, and the male

emerges as a winged insect; probably the male does not overwinter. But the female neither forsakes her bag nor acquires wings, she is impregnated by the male within her bag. Each female produces a large number of small eggs but does not oviposit, for she dies within her bag and her dead body becomes a case for the eggs; at her death her viscera change into a soft cottony mass that acts as a further protection for the eggs. Among some 200 cocoons collected on November 24 I found about half a dozen in which the egg case, the degenerate female, was still living. This species is then a very favorable insect for obtaining eggs and early embryos in large abundance during the colder season of the year, and should prove a valuable object for experimentation.[1]

The controls were kept within their cocoons out-of-doors, and hatched in the end of May. In the experiments sometimes the eggs (in early embryonic stages) were removed from the egg cases, sometimes kept in them.

A. *Experiments with Sunlight*

Direct Sunlight.—Lot no. 77, collected January 4, consisted of egg cases placed in closed dry bottles in the south window of a warm room (21° C.). 77C, kept three weeks in this sunlight, did not hatch; 77A, an untimed period in sunlight, hatched. Lot 78, collected January 4, consisted of freed eggs in corked vials without moisture, with similar exposure to the light; they were divided into four lots, placed in the sunlight for 3, 7, 10 and 14 days respectively, and all hatched about March 1.

Direct Sunlight behind an Alum Heat Filter.—Four lots of freed eggs (nos. 51, 53, 49, 50) collected January 4 were used, placed in the sun behind a heat filter for 2, 7, 18 and 28 days, respectively, and all hatched in January.

[1] A good popular account of this species is given by McCook: "Tenants of an Old Farm," New York, 1885, and this is illustrated with excellent figures. But he makes the common mistake of other naturalists in supposing that the female oviposits. See also Howard and Chittenden, circular No. 97, U. S. Department of Agriculture, 1908.

Diffuse Sunlight.—A considerable number of lots of egg cases and freed cocoons, collected November 4, were placed in diffuse north light in a warm room (21° C.). and all hatched in January and February.

B. *Experiments with Colored Light*

Freed eggs, collected November 4, were placed within vials immersed in colored solutions within larger bottles, the vial passing through the cork of the larger bottle and held by it. The solutions employed were: acid fuchsine in 50 per cent. and 70 per cent. alcohol; Berlin blue in distilled water; safranine O in 95 per cent. alcohol; orange G in 50 per cent. alcohol; eosine in 70 per cent. alcohol; methylen green in distilled water; picric acid in 50 per cent. alcohol; scarlet 12 gm. in 1,000 c.c. water, this last giving monochromatic light.[2]

In Sunlight behind an Alum Filter, then removed to diffuse light in a warm room (21° C.). Lots 43, 46, 47 were immersed in a scarlet solution, as follows:

Lot 43 in sunlight 4 days, hatched January 15.
Lot 46 in sunlight 28 days, hatched January 9.
Lot 47 in sunlight 32 days, hatched January 11.

In Diffuse North Light.—The following experiments were made in a breeding room of which the temperature was a few degrees above that out-of-doors. Two different lots were raised in a fuchsine solution, one in safranine, one in orange G, one in eosine, one in picric acid. All hatched in May.

Others were placed in a room at 21° C. One series were immersed in a fuchsine solution for 7, 18, 28, 35 days, respectively, then removed to ordinary daylight; these hatched in the latter half of January and first half of February. Others were kept continuously immersed in the following solutions: Berlin blue, methyl green, scarlet, and these hatched in the first part of February.

[2] Vide Pennington, W. E., 1897, "A Chemico-physiological Study of *Spirogyra nitida*," Publ. Univ. Penna. Contr. Bot. Lab. 1.

C. *Experiments with High Temperatures*

Freed eggs, from cocoons collected November 4, were placed in an egg incubator at 39° C. for varying periods, then removed to the dark of an ordinarily warmed room (21° C.). Those kept in the incubator for periods of 1, 2, 3, 4, 5, 7 days hatched in February; those kept in the incubator for eight and eleven days did not hatch.

Ten unopened cocoons and ten egg cases placed in a dry covered slide box, and ten egg cases placed in a dry closed jar, all at 32° C., did not hatch. Five egg cases placed in a moist chamber at 28° C. hatched December 15 (these had been collected November 24). Four other egg cases, treated like the last but with less moisture, hatched in January.

D. *Experiments with Low Temperatures*

Six egg cases were placed out-of-doors in a closed tin box, protected from the rain. They hatched, as was to be anticipated, at the same time as the controls.

Fourteen egg cases were placed in a closed jar within an ordinary refrigerator from November 24 until March 29, then removed to a warm room (21° C.); these also hatched at the same time as the controls.

E. *Results of the Experiments*

I tried to raise the small hatched larvæ by placing them upon arbor vitæ within a moist chamber; but owing to the great time consumed in transferring them to fresh pieces of the food plant, I was obliged to relinquish the attempt, and they all died. Consequently I did not determine whether those hatched under the abnormal conditions differ from control larvæ of the same age.

The eggs of this species develop into larvæ under direct sunlight with and without a heat filter, in diffuse light, in all the colored lights employed, at a temperature of 39° C. provided it be not continued longer than seven days, as well as at temperatures at and slightly below freezing. But what seems to be a necessary con-

dition for development is a certain amount of moisture, for the insects die when subjected to higher temperatures within dry vessels. The main effect of increase of temperature seems to be to hasten the rate of development. Probably it is the relative thickness of the chorion of the eggs that proves their chief protection under changed external conditions.

The experiments on this moth and on *Attacus* would show that the cocoon can have no particular value by excluding the sunlight, for we have found that sunlight is not injurious to the eggs and pupæ. Probably the main value of an insect cocoon is that of protecting against enemies, though it may also be of service in preserving a proper amount of moisture; for cocoons soak up the rain and melting snow, and would retain it for a considerable while.

SHORTER ARTICLES AND DISCUSSION

THE ONTOGENY OF A GENUS

In the systematic work of to-day there is noticeable a tendency toward undue magnification of the importance of the smallest units, the species, subspecies, varieties or whatever they are called, to the great detriment of the larger and more important units, the genera, families and higher groups. While there is a very general agreement among systematists as to what constitutes a species or a subspecies or variety, the concept of a genus is found to vary widely; we have not yet brought ourselves to see the necessity of bestowing that care upon the genera which we use in the study of species and minor divisions. Yet after all the genera and the families are the units of paramount importance, for they are the units with which the majority of workers must eventually deal. Zoology has become such a vast field that he who would occupy himself with species must of necessity restrict himself to a very small section of the animal kingdom.

It has therefore become essential for us to examine the characteristics of natural genera, and to analyze them carefully in order that we may discover certain general truths which will aid us in determining what genera are logical and valid and what are mere artificial aggregations, brought together solely for the sake of convenience.

As commonly accepted, a genus is a group of species which is separated from all other similar groups of species by some character common to all the component units, the latter being differentiated *inter se* by the unequal development of the specific, or, more accurately, intergeneric variables. In case a group of species uniformly differs from another similar group in the majority of the characters available for systematic purposes, that group is properly considered a family or a subfamily.

Immediately upon its appearance, a genus (at this stage merely a vigorous species) spreads in every direction just as far as it is possible to maintain itself, that is, until it encounters on every side insurmountable barriers. But the conditions found throughout this habitable area are not uniform. This causes many local races to develop, each grading insensibly into all those surrounding it. Thus a genus in its infancy is in reality a well-marked species, differentiated into many geographical races.

These races do not long maintain themselves in their original relationships. There is somewhere within the range of this young genus, normally at or near the center, an area of optimum conditions, where life is easy and there is no severe struggle for existence. Here various more or less aberrant types arise and are able to perpetuate themselves, spreading out in every direction as did the original stock, but never so far, as they are not so well prepared to encounter adverse conditions. Thus in the second stage a genus is in reality a well-marked species, differentiated into many geographical races, and in the center of its range being accompanied by several additional closely allied species.

After the formation of these several supernumerary species, each usually with a few races of its own, the genus soon reaches maturity. Each of the numerous component forms increases in numbers so that in its own little sphere the struggle for existence becomes acute, and any variation from an arbitrary type is unable to maintain itself. The forms occupying the limits of the range of the genus as a whole (geographical or bathymetrical) are continually trying to colonize new territory, both from their own initiative and as the result of pressure from behind. This encounter with generically unfavorable conditions induces, in the border forms, a more or less pathological condition, inducing great individual variation; and so we normally find that the species which occupy the outer borders of the area inhabited by the genus as a whole, just as in any species the individuals from the edge of the area inhabited by it, are much more variable than those from any other part.

If we take the species of any genus which has reached the stage of maturity just described and arrange them according to the proportionate value of their specific characters, we find in the center a single species, or a group of closely allied species, whose range is coterminal with that of the genus as a whole. This species is, moreover, typically the most variable of any in the genus, and probably is very close to the original stock.

The period of maturity being passed, senescence begins to assert itself. By long existence under fixed conditions the various component species become, as it were, delicate, and are unable to withstand any changes in their environment. Such changes are, however, of constant occurrence, affecting greater or lesser areas; and therefore discontinuance of distribution creeps in, species being cut off from the main zoogeographic area inhab-

ited by the genus, one by one, by the extirpation of the intermediate forms. It often happens, also, that changing ecological conditions at the center of distribution of the genus, such as the local development or introduction of predaceous forms, or of external or internal parasites, destroys the typical form there, leaving only aberrant types; or they may even obliterate all traces of the genus.

Very old genera are thus characterized by having but few species in widely separated localities, each widely different from the others. These are usually (and rightly) regarded as representing a family composed of a few monotypic, or nearly monotypic, genera.

Very often old genera undergo what has aptly been termed an "explosion" of the intergeneric characters, and are then composed wholly, or almost wholly, of curious and eccentric species; again a genus in its senescence often is marked by a great development of certain characters at the expense of others, which usually leads to prompt extinction. In certain localities large numbers of species are remarkable for their eccentric development, and the exaggeration of certain characters out of all proportion to the others, which, so far as we can see, serves no useful purpose. Such localities from a zoological point of view must be considered as old and to have persisted in their present state beyond the normal life cycle of the genera which have given rise to the erratic species. Just as the life cycle of different animals varies enormously, so does that of species and of genera. Scores of genera belonging to the higher groups of the animal kingdom may arise, grow strong, decline, and finally, with a grand "explosion" of their characters, disappear, before a genus belonging to one of the lower groups, of earlier origin, has reached the summit of its strength.

In discussing genera, as well as species, one must always keep in mind that for all animals there are two, and for aquatic animals three types of distribution, viz., (1) geographical, with purely inorganic physical barriers; (2) ecological, with wholly organic barriers, consisting of presence or absence of food and predaceous or parasitic enemies; and (3) bathymetric, again with purely physical barriers of pressure and temperature, the latter commonly being the more important with lower animals, the former with the higher.

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NOTES AND LITERATURE

RECENT CONTRIBUTIONS TO A KNOWLEDGE OF THE EXTINCT AMPHIBIA

The past few months have witnessed an unusual activity among paleontologists in behalf of the extinct Amphibia. There have been several rather extensive papers and an important memoir on the group issued within the last twelve months. It is to be hoped that many other investigators will come to be interested in this group of vertebrates, for it is only by descriptions and discussions that we shall ever attain any adequate conception of the relationships of these highly interesting and important forms. The writer is of the opinion that the present conception is capable of considerable improvement and in order to facilitate this improvement he offers a review of the recent literature on the group.

Dr. A. Smith Woodward (1) has described an interesting new amphibian from the "Oil Shale, at Airly, New South Wales." Dr. Woodward locates his form in the genus *Bothriceps* of Huxley. The skull and greater part of the vertebral column with the ribs and a portion of the right arm are preserved. It is described as a new species under the name *Bothriceps major*, but as this term had already been used by Lydekker for the reception of the uncertain *Petrophryne major* of Owen[1] it will be necessary for the Australian specimen to receive a new name, for which the term *Bothriceps woodwardi* would not be inappropriate. Dr. Woodward allies the form with the Archegosauridæ, but the reviewer is rather inclined to think that the Tuditanidæ would be its nearer relatives. This is the third form described from the Hawkesbury formation of New South Wales. Further search will undoubtedly reveal other Paleozoic amphibia. It will be noticed in this as in so many other Paleozoic localities where fossil amphibia are found, that nearly every new specimen represents an unknown form, thus indicating the diversity and age of the group. The known species from the Hawkesbury formation are: *Bothriceps australis* Huxley, *Bothriceps woodwardi* and *Platyceps wilkinsoni* Stephens.

Dr. S. W. Williston has described in some detail (2) the

[1] Cat. Fossil Amphb. and Rept. Brit. Museum, Pt. IV, p. 174.

remains of *Dissorophus multicinctus* Cope which has recently been recovered from the reputed Permian of Texas. His material greatly increases our knowledge of the genus and of the anatomy of the Permian amphibia. He describes a complete skull, in which, unfortunately, the sutures are not discernible. Nor are the lateral line canals to be found, a fact to be regretted since we shall undoubtedly be enabled to base considerable importance on these structures did they occur. The skull roof is pitted like all other of the Permian amphibia from Texas. A large portion of the carapace is described with its attached vertebræ. The dermal shield is broad, continuous and pitted, forming a covering over the thoracic region of the animal. Limb bones, a scapula and a portion of the interclavicle are described. The form is closely related to another animal recently described by Dr. Williston and the two are placed in the new family Dissorophidæ. The paper closes with a taxonomic list of the Permian amphibia from Texas for which paleontologists will be grateful. There are three orders, nine families and thirty-four species so far known in the fauna.

The same writer has described (3) a nearly complete skeleton of a new temnospondylous amphibian from the Texas Permian. The form is very remarkable in several of its characters. The following are the chief unusual characters of the new genus: a median unpaired rostral opening leading into a palatine vacuity, greatly enlarged antorbital vacuities, temporal fenestræ, apparent absence of the parasphenoid bone, osseous carpus and tarsus and the possession of short heavy ribs borne on transverse processes. The skeleton is greatly similar to that of *Eryops*, but the skull shows decided differences.

The temporal fenestra is not homologous to the superior temporal fenestra of reptiles, but it is rather to be considered as a greatly elongate and closed epiotic notch. The median unpaired rostral opening is similar in structure to the one found in the skull of *Dasyceps bucklandi* Lloyd from the Permian of Kenilworth, though in the present form the opening is much further forward and smaller. The antorbital vacuities in the present form, on the other hand, are much larger than the same openings in *Dasyceps*.

Dr. Williston was able to make out the complete anatomy of the skull and has figured it in three views. The most remarkable feature of the palatal structure is the apparent absence of the parasphenoid. The vertebral formula is 22 for the presacral vertebræ, an uncertain number of caudals and a single sacral. The

sacral rib is much like that of *Eryops* in which the structure takes a very unusual form for a rib. The phalangeal formula for the foot is 1, 2, 3, 4, 2. The complete number of digits in the hand is not preserved. The carpus has nine possibly eleven osseous elements, and the tarsus has twelve osseous elements.

The paper is well illustrated. There is a restoration of the skeleton of *Trematops milleri* and an outline drawing of the scapula of *Eryops latus* Case. The new genus *Trematops* is the type of a new family Trematopsidæ in which the form described by Cope as *Acheloma cumminsi* is doubtfully associated.

The same writer (4) has redescribed from more complete material the species named by Cope as *Diplocaulus limbatus* from the Permian of Texas. The paper is based on several more or less incomplete skeletons. These include several additional features to our knowledge of the anatomy of the peculiar Diplocaulidæ. Limbs have heretofore been unknown in the group although their presence has been suspected from the presence of pectoral girdles preserved with some specimens. Dr. Williston, however, for the first time actually describes well-formed limb bones for the group. The humerus is very remarkable in that it has an epicondylar foramen, a character known in only one other amphibian, *Acheloma*. The complete morphology of the skull with the exception of some features of the palate are made out and represented in two plates. The clavicular girdle, mandible, vertebræ and limb bones are represented in other plates. The paper concludes with remarks concerning the relationship of the group to which *Diplocalus* belongs and associates the Oklahoma Permian form *Crossotelos* with the *Diplocaulus*. He remarks that in the Microsauria the capitulum of the rib is always attached intercentrally and suggests that *Diplocaulus* must be retained among the Microsauria.

The same writer (5) has given an extensive paper on new Permian forms in which he describes a new genus and species of amphibia under the name *Cacops aspidephorus*. This form he locates in the family Dissorophidæ. The paper opens with a brief discussion of the "Character of the Permian Beds of Northern Texas," "Conditions of Fossilization" and "Associated Vertebrates." The form described in the paper is represented by a skeleton which is remarkably complete "with no more plaster in its construction than was necessary to cement the freshly broken parts . . . save of many of the phalanges. . . ." It was so complete and well preserved as to be capable of being mounted like a recent skeleton which has been well executed by

Mr. Paul Miller with remarkable success. A photograph of the mounted skeleton is given in one of the plates.

There are four skulls. The most remarkable feature of the dorsum is the presence of a closed otic notch which resembles a temporal fenestra. In none of the skulls was it possible to determine the sutures and the structure of the skull had to be determined more by topographic features. The structure of the palate is of the stegocephalian type, though remarkable in some of its features, such as the large size of the palatal openings. The vertebræ were preserved practically complete and the vertebral formula is—presacral, 21; sacral, 2; pygals, 6, and chevron caudals, 15 or 16. Fifteen of the vertebral spines are elongated and expanded and serve to support a carapace of shield-shaped, scute-like plates which overlap shingle-like. They greatly resemble in structure the dermal plates of *Dissorophus*. A discussion of the "carapace in allied forms" is given and the dermal elements of *Aspidosaurus*, *Zatrachys*, *Dissorophus* are discussed. Plates are suggested by the expanded neural spines of *Euchirosaurus* and *Eryops*.

The vertebral column is fully discussed. This includes some unusual features, such as two sacral vertebræ and a well-preserved atlas which is composed of a single piece. The writer discusses also the significance of the hypocentra and pleurocentra, one of the most perplexed questions in connection with the extinct amphibia. The pectoral girdle consists of the fused scapula-coracoid, a cleithrum, clavicles and interclavicle. The humerus and its use in diagnosis is discussed at some length. Among the material studied are many humeri, some of which suggest unknown forms of amphibia. Two new families, the Trematopsidæ and Dissorophidæ, are proposed and the characters given. The paper closes with a discussion of the restoration of *Cacops* and the description of a peculiar form of reptile in which the vertebræ are intermediate between what is known in temnospondylous amphibia and reptilia.

The same writer (16) in a discussion of the faunal relations of the early vertebrates, presented before Section E of the American Association in 1909, gives the relations of the American Permian and Carboniferous amphibian faunas with those known elsewhere. He reaches the conclusion that the Permian fauna is especially isolated. In his discussion of the Microsauria he says, "It has been assumed on entirely insufficient evidence that they too were all amphibians"—and later: "We may be assured that some of them before the close of the Pennsylvanian were inhabit-

ants of high-and-dry land regions where fleetness of movement, rather than obscurity, preserved them from their enemies, crawling reptiles in everything save some insignificant technical details of their palates.'' This has been recognized by many students of the fossil amphibia and Gadow placed them in a new group which he has called Proreptilia, but his classification does not seem to have been accepted. Dr. Williston says further, ''Specialization of the microsaurs had reached the extraordinary extent of snake-like limbless forms.'' These snake-like forms have been usually associated in another order, the Aistopoa, but the reviewer has shown elsewhere that the group is a heterogeneous one and is made up of specialized microsaurian forms of diverse relationships.

Dr. E. C. Case (6) has described three, perhaps four, new forms of amphibia from the Permian of Texas. The forms as a whole are very insufficiently described. One species, *Trimerorhachis alleni* is described in ten lines and no figure given. This manner of descriptions should be subjected to the severest criticism as it imposes many heavy burdens on the shoulders of succeeding workers. The new genus *Tersomius* is not defined at all. While we may not doubt that the genus is new, judging from the single outline figure, yet it would have been much better, for those who are not so well acquainted with the Permian fauna as is Dr. Case, had he given in what ways it differs from the other amphibia. He allies the genus with *Trimerorhachis* at least so far as resemblances are concerned. The new genus and species are given in fifteen lines of less than ten words each.

A new form, *Gymnarthrus willoughbi*, is much better described. Its relations are uncertain. Dr. Broom allies it with the amphibia, but Dr. Case does not regard the form as such. He remarks its close alliance with *Cardiocephalus sternbergii*, which is amphibian. If *Gymnarthrus* is not amphibian it is certainly a very remarkable amphibian-like reptile.

Dr. E. B. Branson (7) has described and figured, in an excellent photograph, footprints of possible amphibians from the Mississippian rocks of Giles Co., Virginia. Five well-preserved tracks are represented in the figure. The author proposes the new specific name *Dromopus aduncus* and gives a list of the amphibian footprints known from the Mississippian.

The most notable attempt on the part of paleontologists, to elucidate an entire amphibian fauna, is that of Armand Thevenin (8) in the most important memoir on fossil amphibia for many months. The National Academy of France awarded him a prize

for the presentation of the memoir. The paper was published in successive issues of the *Annales de Paleontologie* and in complete form contains sixty-three quarto pages and nine photogravure plates, illustrating all that is known of the Paleozoic amphibian fauna of France up to the present.

The author divides the amphibian forms into four groups: the Phyllospondyles, which is a subordinate group of the "Stegocephales"; the Temnospondyles: the Aistopodes, and the Microsaurians, which unfortunately he ranks in with the reptiles, and describes under this heading a form which a few years ago he had concluded was a rhynchocephalian. Dr. Williston was more inclined to regard it as a Cotylosaurian. Whatever reptilian group it belongs to the reviewer is unable to say, but he is quite certain it is not a Microsaurian.

Dr. Thevenin discusses, under the heading, Phyllospondyles, the forms *Protriton fayoli* Thevenin, *P. petrolei* Gaudry, and *Pelosaurus laticeps* Credner. The second group consists of *Actinodon brevis*, *A. frossardi* and *Euchirosaurus rochei*. The Aistopodes are represented by a single new form which is unnamed. The specimen strikingly suggests the snake-like amphibians of Ohio and Ireland. There are no true representatives of the Microsauria known in France.

Our author discusses some general questions in regard to the amphibia, such as—"the relations of the Autun amphibia to those of other countries," "the homologies of the temnospondylous and the phyllospondylous vertebræ," "homologies of the elements of the pectoral girdle," "the ancestry of the Stegocephalia" and "the descendants of the Permian Stegocephalia."

Nothing new is added to our previous knowledge of the complex relations of the elements of the temnospondylous vertebra, which is one of the most vexed and most discussed questions in connection with the extinct amphibia. His homologies of the elements of the pectoral girdle are the ordinary interpretations. The ancestors of the Stegocephalia are possibly the crossopterygian fishes, although this is no new conclusion nor does our writer claim this. Perhaps the crossopterygians will do as well as anything. At least they will serve until we find what the *real* ancestors were.

In a discussion on "the descendants of the Permian Stegocephala" he concludes that the branchiosaurian forms were the ancestors of the modern Urodeles and that the Temnospondylia gave rise to some of the reptiles, possibly some of the Cotylosauria. Our author, on a later page, gives the stratigraphic dis-

tribution of the amphibians and reptiles of the Permian of France. His final conclusion is that the diversity of the reptiles and amphibians shows that the groups had arisen long previously and the existence of similar forms in Europe and America would indicate some land connection of the two continents during the Permian.

Dr. Friedrich von Huene has redescribed the skull of *Dasyceps bucklandi* (Lloyd) (9) from the Permian of Kenilworth. This skull was previously studied by Huxley, but rather inadequately described. After a careful description of the elements of the skull Dr. Huene locates the form in the family Melosauridæ, although the form has characters which are unusual for the other members of this group. He discusses the character and significance of the "facialgrube" or internasal opening, which has been described in another Permian form by Williston. Huene finds the same opening occurs in many living urodeles and lists nineteen species in which the opening has been described. He says that it has also been observed in certain members of the Permian Microsauria described by Fritsch from Bohemia. Its significance is possibly the same as in the living amphibia, that of receiving the glandula intermaxillaris. Since this gland in living land-dwelling amphibia secretes a sticky substance used in capturing insects, Dr. Huene suggests that perhaps *Dasyceps* also captured insects. This may, of course, have been possible, but to the reviewer it suggests a greater activity than could be expected of such a sluggish creature as *Dasyceps* undoubtedly was, since it would require many insects to feed an animal three or four feet long and it would be necessary to secure them in some quantity. Dr. Huene suggests that the insects "im Perm und Carbon sehr bedeutende Grössen erreichten"; such was undoubtedly the case with a few species, but the great majority of insects of the Carboniferous and Permian do not greatly exceed the modern insect fauna, so that Dr. Huene's argument on that score is not a good one. *Dasyceps* was probably a land animal and Dr. Huene thinks this is indicated by the presence of the internal opening which occurs only in the land-inhabiting forms among recent Amphibia. Perhaps the analogy may be carried so far.

Dr. R. Broom (10) compares the Permian amphibian fauna of North America and Europe and finds little similarity. He regards the American types as more highly developed. He divides the Permian amphibia of North America into four groups.

He discusses again the relationship of *Lysorophus* and in his discussion quotes the reviewer as saying what he did *not* say. The point of the reviewer's criticism of the reference of *Lysorophus* to the Urodela was *not* the presence of ribs nor yet the snake-like character which Dr. Broom explains in a very elementary way, but it was the *character* of the ribs. Their long, curved condition is unknown among other Caudata and the reviewer does not feel satisfied that *Lysorophus* is a Urodele even though limbs should be discovered.

Dr. Broom suggests for the newly described *Gymnarthrus* of Case an amphibian relationship. The dorsum of the skull shows characters, however, which apparently ally it with *Pariotichus*.

Dr. Broom's other essay (11) on practically the same subject matter gives the additional suggestion that the American and African amphibia are "two different modifications of the same earlier fauna.'

Mr. Robert Dunlop (12) has given some interesting notes on Carboniferous and other Paleozoic amphibia of Scotland contained in the Kilmarnock Museum before they were destroyed by fire. His notes are accompanied and illustrated by two excellent half-tone plates of photographs of type specimens of *Loxomma*, *Pteroplax* and *Anthracosaurus*, all of which is very welcome information.

Jaekel (14) has proposed a new classification for the Chordata which he calls Vertebrata. He divides the "Stamm" into three subgroups Tetrapoda, Pisces and Tunicata, and makes no allowance for amphioxus. He proposes two new classes of "Tetrapoda," Hemispondyla and Microsauria with the ordinary classes Amphibia, Reptilia, Aves and Mammalia. The forms he groups in his new class Hemispondyla are the branchiosaurs and a new group which he calls Sclerocepholi. Dr. Jaekel has made several bad blunders in this classification. The first one is to separate the branchiosaurs from the Amphibia, to which they belong without the slightest shadow of a doubt. The next one is the alliance of *Amphibamus* to the Branchiosauridæ, to which it is not so closely allied as it is to the Cotylosauria. *Amphibamus* is far removed in structure from the Branchiosauridæ. His next error is the inclusion of *Acanthostoma* in the same group with the Branchiosauridæ. Their structures do not indicate relationships at all.

His class Microsauria is wholly untenable, as Dr. Williston well says (17). The group which we call Microsauria now will undoubtedly require revision and it looks as if it were going to get

it, but that the animals now included in that group represent a class distinct from all other vertebrates I, for one, will not for a moment concede.

The fundamental error made by Dr. Jaekel, as the reviewer sees it, is the attempt to base a classification of vertebrates on a single character. This has always failed in the the past and must, in the nature of the case, fail in the future; since classification, if it is to mean anything, must take into consideration the entire organization. The paper is full of many other smaller errors, errors of knowledge and errors of judgment. One of these errors is relating such widely distinct forms as *Ceraterpeton* and *Diplocaulus*.

The same author has given a study of the limbs of the oldest vertebrates in which (15) he attempts to sustain his classification, but his facts and arguments are not at all convincing and the paper is little more than a republication of parts of the essays of other investigators.

Dr. Williston (17) has recently published another essay on the Permian fauna of Texas in which he gives especially a study of the vertebræ and adopts the view of Cope as to the ultimate fate of the elements of the rhachitomous vertebra. He regards *Eosauravus copei* Will. (*Eosauravus punctulatus* (Cope)) as allied to *Hylonomus* and for that reason "the oldest known reptile" is a microsaur. Just what his reasons for this alliance are he does not say. In the present imperfect state of our knowledge of *Hylonomus* and its Canadian brothers such a reference would be very uncertain. In the last paragraph he records the interesting discovery of limbs in *Lysorophus*.

A general review of the above essays shows that more than half of them represent pioneer work, that is, descriptive and classificatory investigations. Five of the essays bear more largely on the faunal relations as exhibited by the Amphibia. One gives us new light on the significance of a structure found in the ancient forms. This is where work is greatly needed. Our knowledge of the ancient amphibian fauna will increase as time goes on but the greater part of the pioneer work is already done. The way is now open for some good investigations on the structure of the ancient Amphibia and the meaning of these characters as interpreted in the light of modern comparative anatomy and embryology.

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Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

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AMERICAN NATURALIST

VOL. XLV *July, 1911* No. 535

GERM-CELL DETERMINANTS AND THEIR SIGNIFICANCE[1]

PROFESSOR R. W. HEGNER

UNIVERSITY OF MICHIGAN

INVESTIGATIONS of the origin of the germ cells in a number of animals have brought forth certain phenomena which indicate that these cells are determined as such at a very early period in embryonic development, and that in some cases the material which apparently determines the germ cells is visible at this time. Conclusions can be drawn from these observations which are of considerable interest.

The frequently repeated statement that the germ cells are derived from the mesoderm or from the entoderm is of course erroneous in those instances where the germ cells can be identified before the formation of the germ layers, and it seems probable that the primary cell differentiation, *i. e.*, the separation of the germ cells from the somatic cells, takes place at an early period in the embryonic development of even those animals where this has not been actually observed. A few of the most pronounced cases of the early differentiation of germ cells are briefly described in the following paragraphs and several general conclusions arrived at from this evidence.

The best known example is *Ascaris*, as described by

[1] Contributions from the Zoological Laboratory of the University of Michigan, No. 135. From a paper read before the Research Club of the University of Michigan, November 9, 1910.

Boveri ('92). The first cleavage division of the egg of *Ascaris* results in two daughter cells, each containing two long chromosomes (Fig. 1, *A*). In the second division the chromosomes of one cell divide normally and each daughter cell receives one half of each (Fig. 1, *B, s*). The chromosomes of the other cell behave differently; the thin middle portion of each breaks up into granules

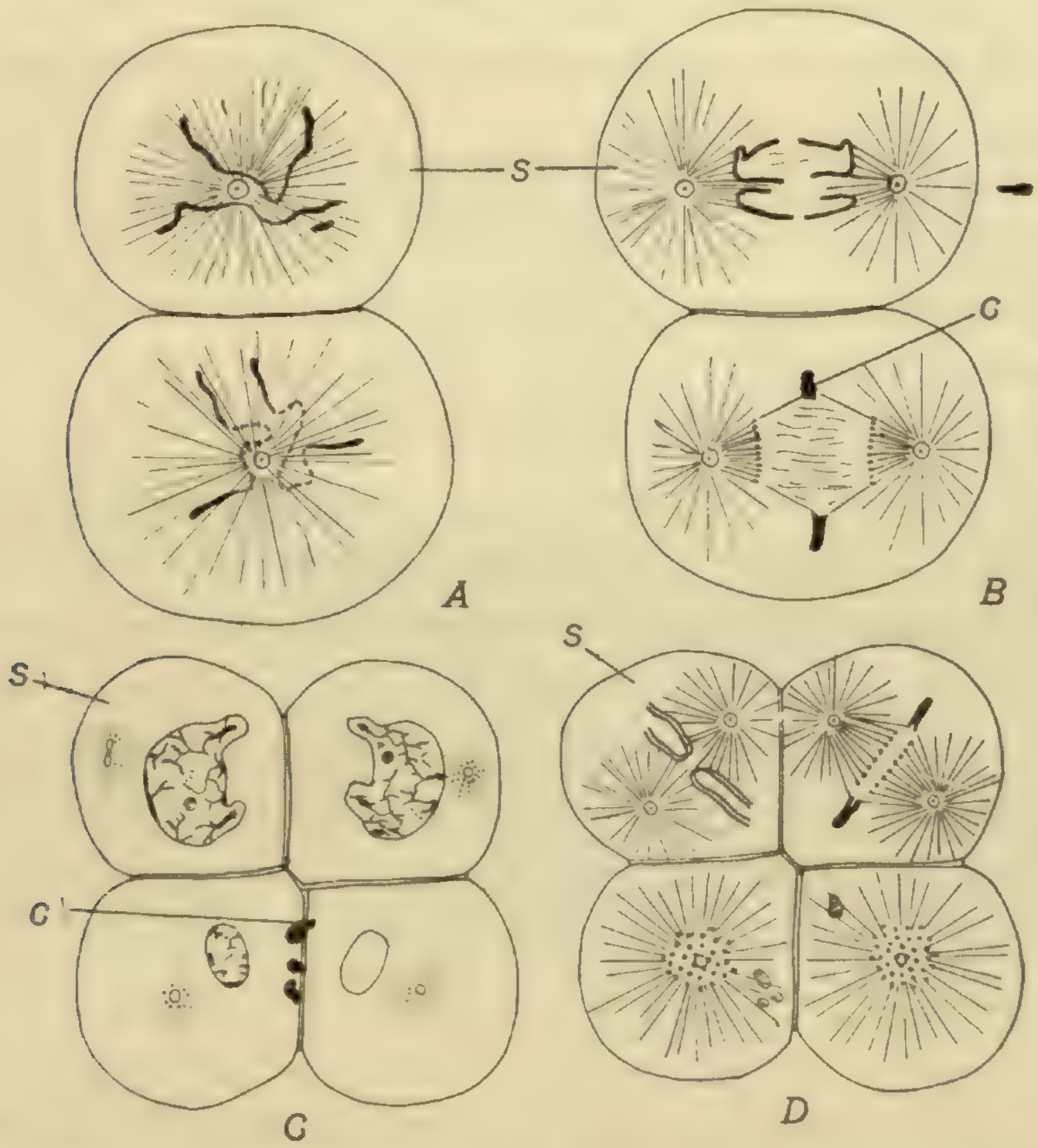

FIG. 1. Origin of the primordial germ cells and casting out of chromatin in the somatic cells of *Ascaris*. (From Wilson's cell, after Boveri.) *A*, two-cell stage dividing; *s*, stem-cell, from which arise the germ cells. *B*, the same from the side, later in the second cleavage, showing the two types of mitosis and the casting out of chromatin (*c*) in the somatic cell. *C*, resulting four-cell stage; the eliminated chromatin at *c*. *D*, the third cleavage, repeating the foregoing process in the two upper cells.

(Fig. 1, *A*) which split, half going to each daughter cell, but the swollen ends (Fig. 1, *B*, *c*) are cast off into the cytoplasm. In the four-cell stage there are consequently two cells with the full amount of chromatin and two with a reduced amount. This inequality in the amount of chromatin results in different sized nuclei (Fig. 1, *C*); those with entire chromosomes (*s*) are larger than those that have lost the swollen ends (*c*). In the third division

one of the two cells with the two entire chromosomes loses the swollen ends of each; the other (Fig. 1, *D*, *s*) retains its chromosomes intact. A similar reduction in the amount of chromatin takes place in the fourth and fifth divisions and then ceases. The single cell in the thirty-two-cell stage which contains the full amount of chromatin has a larger nucleus than the other thirty-one cells and gives rise to all of the germ cell, whereas the other cells are for the production of somatic cells only.

The primordial germ cell of *Ascaris*, therefore, contains two entire chromosomes; every other cell possesses two chromosomes which have lost part of their substance. In other words, the germ cells possess a certain amount of chromatic material not present in the somatic cells.

There is also an early differentiation of the germ cells in the fresh water crustacean, *Cyclops* (Haecker, '97). According to Haecker, "Aussenkörnchen" arise at one pole of the first cleavage spindle (Fig. 2, *A*, *ak*); these

FIG. 2. Origin of the primordial germ cell in *Cyclops*. (From Haecker.) *A*, the first cleavage division, showing the "Aussenkörnchen" (*ak*) at one pole of the spindle. *B*, the thirty-two-cell stage; the primordial germ cell (*Kz*) contains all of the "Aussenkörnchen" (*ak*).

are derived from disintegrated nucleolar material and are attracted to one pole of the spindle by a dissimilar influence of the centrosomes. During the first four cleavage divisions the granules are segregated always in one cell (Fig. 2, *B*, *kg*); at the end of the fourth division these "Aussenkörnchen" disappear, but the cell which contained them can be traced by its delayed mitotic phase and is shown to be the primordial germ cell.

In this case, as in that of *Ascaris*, the primordial germ cell and the germ cells derived from it possess certain nuclear materials not present in the somatic cells. The

latter seem to be limited because of their absence to the performance of vegetative functions, and the germ cells appear to have the power of reproduction because of their presence.

A recent paper by Elpatiewsky (1909) deals with the early embryonic development of the arrow worm, *Sagitta*. This investigator finds that, at the stage when the two pronuclei are in the center of the egg, a body appears at the vegetative pole lying near the periphery (Fig. 3,

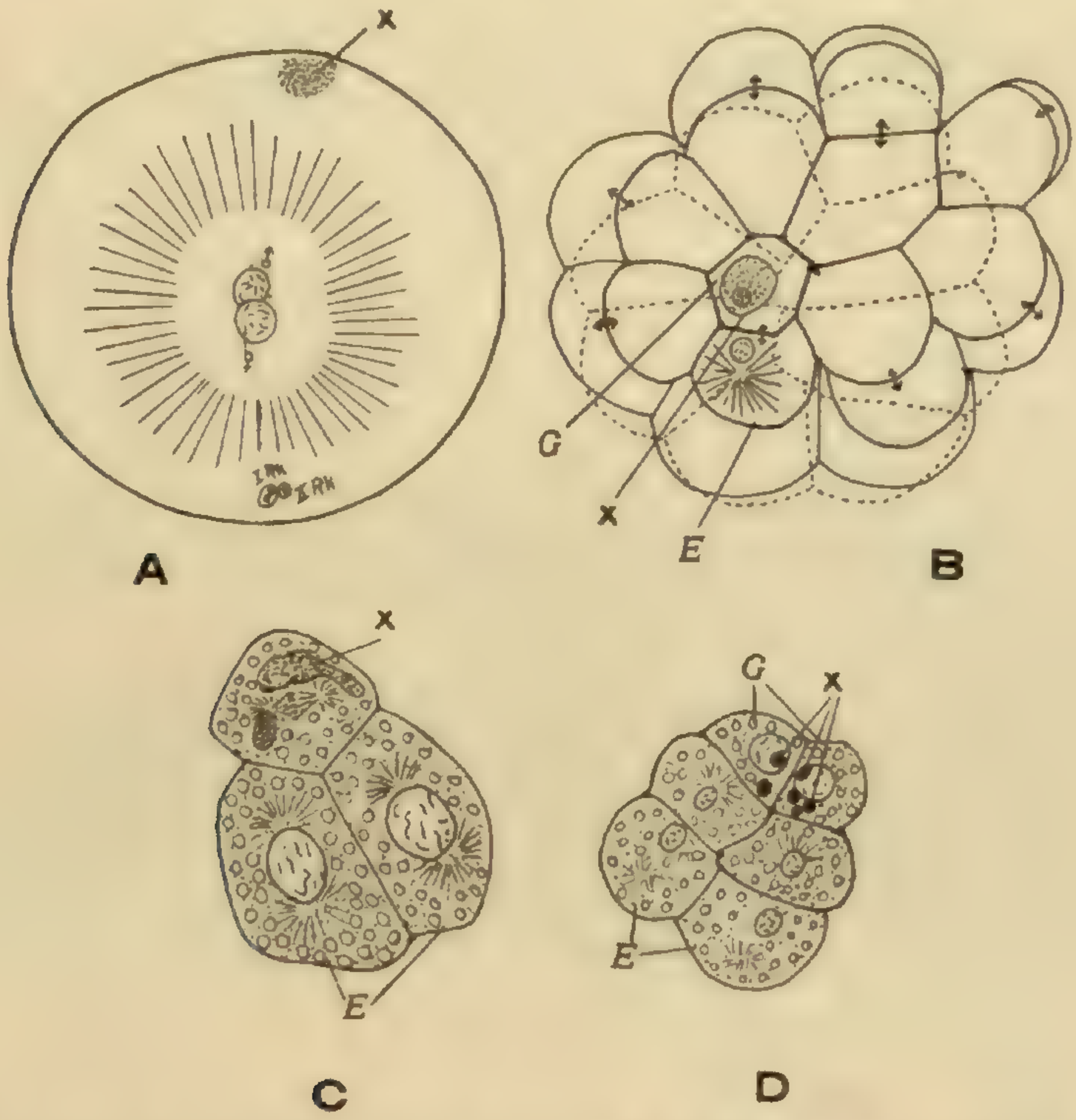

FIG. 3. Origin of the primordial germ cells in *Sagitta*. (From Elpatiewsky.) *A*, egg with conjugating pronuclei; polar bodies (*I Rk.* and *II Rk.*) and "besonderer körper" (*x*) embedded in cytoplasm. *B*, thirty-two-cell stage: the primordial germ cell (*G*) contains the "besonderer körper" (*x*); entoderm cell at *E*. *C*, the primordial germ cell dividing; the "besonderer körper" (*x*) within it is also dividing; the entoderm cell has already divided (*E*). *D*, two germ cells (*G*) resulting from the first division of the primordial germ cell; each contains part of the "besonderer körper" (*x*).

A). This body, which is termed "besondere körper," consists of coarse granules which do not stain quite so deeply as the chromosomes. During the first four cleavage divisions the "besondere körper" does not divide, but is always to be found in one blastomere. In the fourth division the blastomere which contains this body divides unequally; the larger cell is destined to produce the entoderm (Fig. 3, *B*, *E*); the smaller cell, which con-

tains the "besondere körper" is the primordial germ cell (Fig. 3, *B, G*). The first division of this primordial germ cell (Fig. 3, *C*) results in two daughter cells, one of which obtains a larger portion of the "besondere körper" (*X*) than the other (Fig. 3, *D*). This is interpreted as the differential division, the cell which possesses the larger amount of the divided "besondere körper" giving rise to the male germ cells, the other to the female germ cells in the hermaphroditic adult. The "besondere körper" now gradually becomes paler and finally disappears. Buchner ('10) and Stevens ('10) have confirmed Elpatiewsky's observations. The origin of the "besondere körper" was not determined.

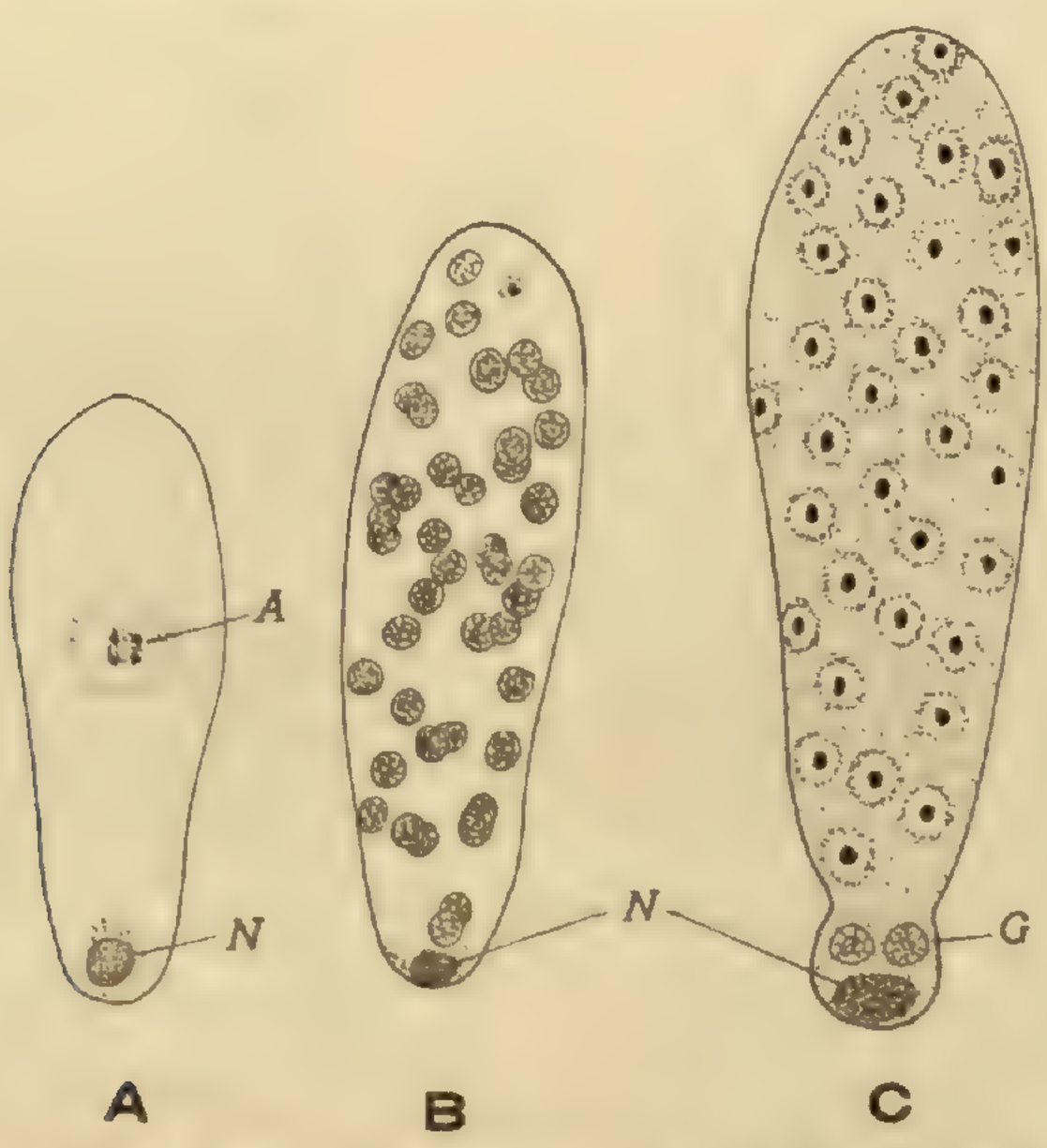

FIG. 4. Origin of the primordial germ cells of *Oophthora*. (From Silvestri.) *A*, the nucleolus (*N*) of the germinal vesicle (*A*) has passed to the posterior end of the egg. *B*, an egg containing a number of cleavage nuclei. *C*, the cells which come under the influence of the nucleolus (*N*) become the primordial germ cells (*G*).

These investigations show the germ cells of *Sagitta* to be similar to those of *Ascaris* and *Cyclops* in that they contain a darkly staining material not present in the somatic cells.

In *Oophthora* and other parasitic hymenoptera, Sylvestri ('09) finds that the nucleolus of the germinal vesicle passes to the posterior end of the egg during maturation (Fig. 4, *A*). Here it remains until the cleavage nuclei reach the periphery (Fig. 4, *B*). The cells which then come under the influence of the nucleolus be-

come the primordial germ cells (Fig. 4, *C*, *G*) and give rise to the germ glands of the adult. The similarity between this process and that described for *Ascaris*, *Cyclops* and *Sagitta* is obvious.

Finally in chrysomelid beetles the primordial germ cells are differentiated at a very early period (Hegner, '09). At the posterior end of the eggs of *Calligrapha multipunctata* and allied species there is a disc-shaped mass of granules which stain like chromatin. I have called this the pole disc (Fig. 5, *A*, *gc. d*). When the cleavage nuclei reach the periphery of the egg they fuse with the superficial layer of cytoplasm everywhere except at the posterior end; cell walls then appear and a blastoderm is formed. When the cleavage nuclei which reach the posterior end of the egg encounter the pole disc granules they gather these granules about them and continue their migration (Fig. 5, *B*, *gc*); cell walls are formed, and they finally come to lie entirely outside of the egg (Fig. 5, *C*, *gc*).

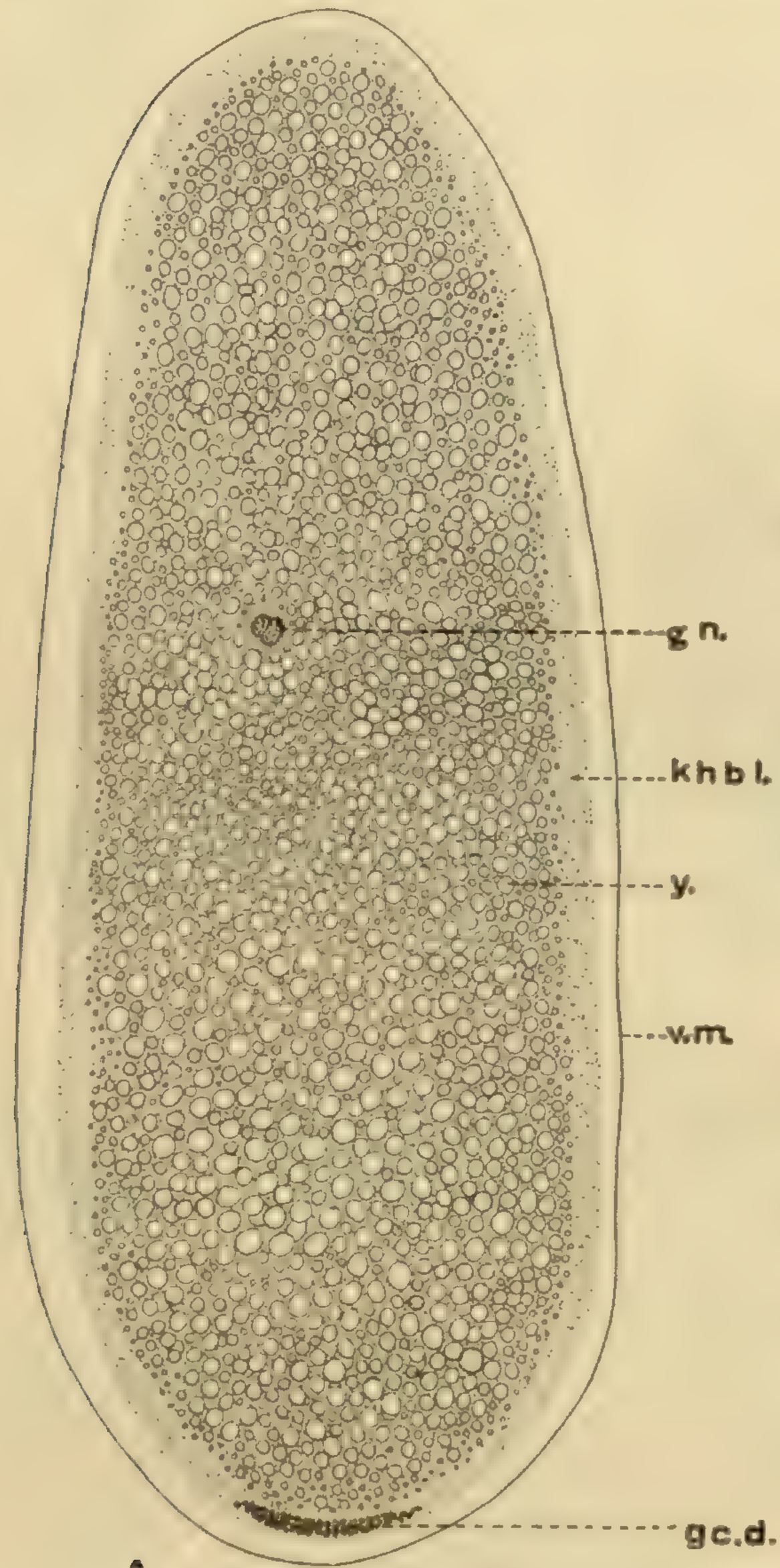

FIG. 5.

There are sixteen cells which separate from the egg in this manner, and they take out of the egg with them practically all of the pole disc granules (Fig. 5, *C*, *pd.g*). These sixteen cells divide to form thirty-two; in this division apparently one half of the granules contained in each cell pass to each of the daughter cells (Fig.

5, *D*, *pd.g*). A second division results in sixty-four cells; this number is constant until a late stage in embryonic development.

These sixty-four cells have been traced through the early embryonic stages. First they migrate back into the egg through a "pole cell canal" (Fig. 5, *C*, *pc*) sit-

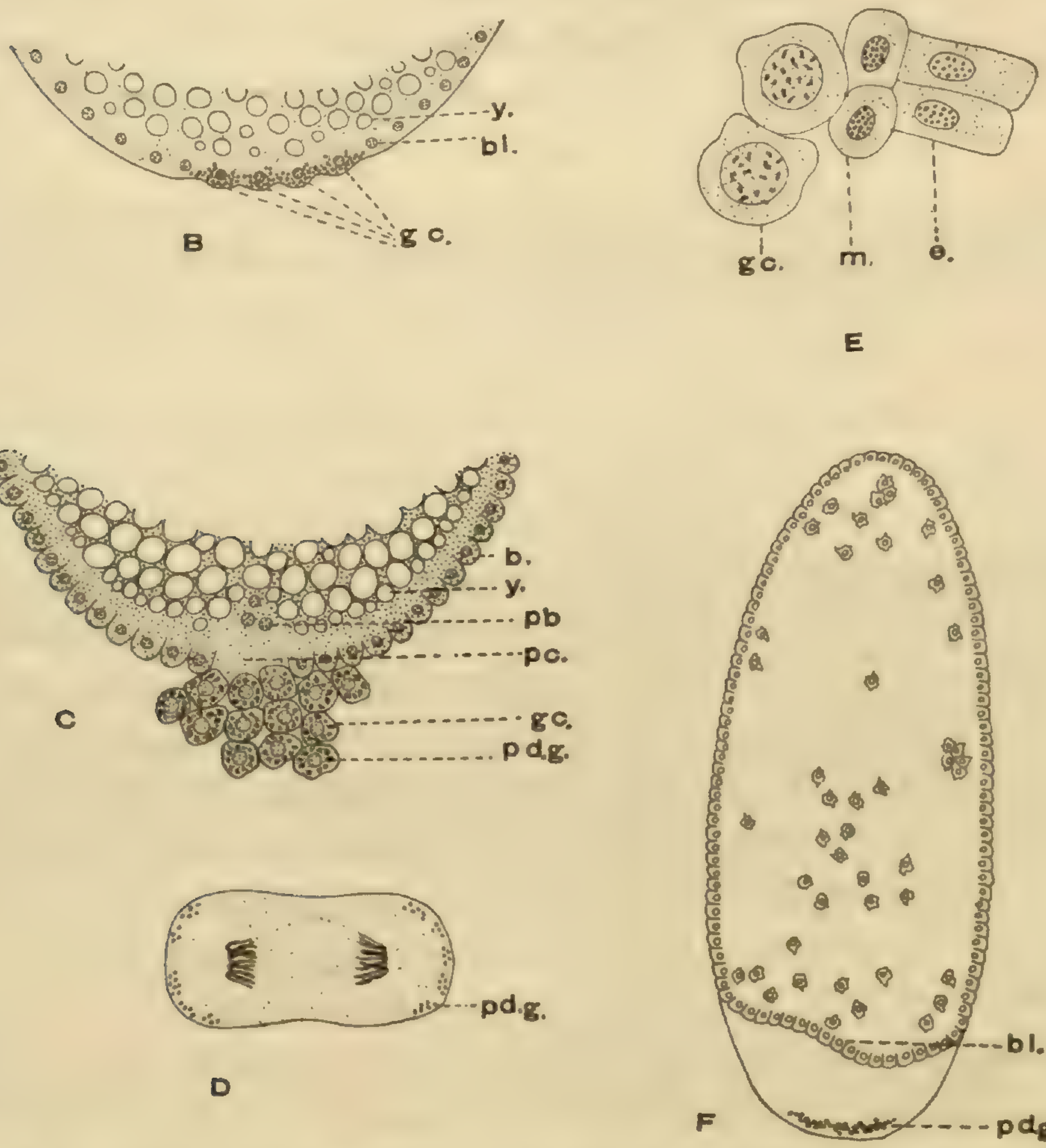

FIG. 6. Origin of the primordial germ cells in chrysomelid beetles. *A*, longitudinal section through a freshly laid egg of *Calligrapha bigsbyana*, showing pole disc (*gc.d*) at posterior end. *B*, longitudinal section through the posterior end of an egg of *C. multipunctata* eighteen hours after deposition, showing pole disc granules within the primordial germ cells (*gc*). *C*, longitudinal section through the posterior end of an egg of *C. bigsbyana* twenty-four hours after deposition, showing the primordial germ cells containing pole disc granules (*pd.g*). *D*, a primordial germ cell of *C. multipunctata* in anaphase of mitosis; the pole disc granules (*pd.g*) are apparently equally distributed at either end. *E*, two germ cells (*gc*) and neighboring mesoderm cells (*m*) and ectoderm cells (*e*) from an embryo of *C. multipunctata*. *F*, longitudinal section through an egg of *Leptinotarsa decemlineata* twenty-four hours after the posterior end had been killed with a hot needle, thus preventing the pole disc granules (*pd.g*) from taking part in the development. No germ cells are formed (compare with *C*). *bl* = blastoderm; *e* = ectoderm cell; *gc* = germ cell; *gc.d* = germ cell determinants; *gn* = conjugating pronuclei; *khbl* = keimhautblastem; *m* = mesoderm cell; *p* = posterior end of egg; *pbl* = pseudoblastodermic nuclei; *p.c* = pole cell canal; *pd.g* = pole disc granules; *vm* = vitelline membrane; *y* = yolk.

uated near the posterior end of the ventral groove. Then they separate into two apparently equal groups, one on either side of the embryo, which are soon recognizable as the two germ glands.

Because only those cells which gather in the pole disc granules become germ cells, I have called these granules "germ cell determinants" (Hegner, '08). This term has been objected to by Wieman ('10) because "the term implies the attribute of certain potentialities that these granules have not been shown to possess" (p. 180). The morphological evidence is, I believe, strong enough to warrant the use of the term; recent experiments, however, add to the convincing facts already published (Hegner, '08, '09). It is possible to show that if the pole disc is prevented from taking part in the development of the egg, no germ cells will be produced. Attempts to extract the pole disc by means of pricking the freshly laid egg and allowing them to flow out were only partially successful (Hegner, '08). A new method was later employed which absolutely prevented the cleavage nuclei from encountering the pole disc. In these experiments the posterior end of the egg was touched with a hot needle and that portion containing the pole disc was killed. In every instance the development continued and in the eggs so far examined the blastoderm formed normally over all of the surface except at the posterior end; here it was built at the end of the living substance as shown in Fig. 5, *F*, *bl*. No germ cells were produced. I conclude from this that the pole disc granules *are* necessary for the formation of germ cells, and that they are really "germ cell determinants." Of course it might be argued that some other substance lying at the posterior end of the egg is responsible for the differentiation of the germ cells, but this seems highly improbable. Wieman ('10) states that in *Leptinotarsa signaticollis*, a species I have not studied, "the granules are not all taken up by the cells in their migration and the greater part of them remains behind after the cells have passed through" (p. 186). This is certainly not the case in the many eggs that I have examined, and a reexamination

shows that only a few of the pole disc granules remain in the egg after the germ cells are formed, as was clearly pointed out in a former paper (Hegner, '09, Plate II, Fig. 16).

The origin of the pole disc granules is not known. It seemed to me probable that they came from the nucleus of the egg just before maturation and consisted of nuclear material. This conclusion was reached (1) because these granules stain like chromatin, (2) because in many insects the nucleus of the oogonium casts out chromatic material (Nebenkerne), and (3) because the substance which determines the germ cells in *Ascaris*, *Cyclops* and *Oophthora* is of nuclear origin, and in one case (*Ascaris*) is chromatin. Wieman believes that "the granules of the pole disc consist of particles derived from the food stream of the ovum that form an accumulation in the protoplasm in its posterior part" (p. 187). This possibility was pointed out in a former paper (Hegner, '09, p. 274), a fact Wieman seems to have overlooked. It was also suggested in the same place that if the granules are derived from the nurse cells they probably come from the nuclei of these cells. The pole disc granules gradually disappear after the germ cells are formed.

It may be of interest to mention the results of operations performed upon eggs in which the germ cells had already differentiated at the posterior end (Fig. 5, *C*). Such eggs, when touched with a hot needle, continued to develop, and produced embryos and larvæ without germ glands. This I believe is the earliest stage on record on which surgical castration has been performed.

The visible presence of germ cell determinants in the primordial germ cells of the animals described above suggests two possibilities as to their importance: (1) They may represent idiochromatin, *i. e.*, germ plasm, or (2) they may influence the metabolism of the cells and thus determine their character.

1. The history of the germ cells in chrysomelid beetles illustrates in a remarkable way the theory of germinal continuity as expressed by Weismann ('04). Weismann believes with Nägeli that "there are two great categories

of living substance—hereditary substance or idioplasm, and 'nutritive substance' or trophoplasm, and that the former is much smaller in amount than the latter'' (Weismann, '04, Vol. I, p. 341). The idioplasm of the germ cells he calls germ plasm, a substance which is ''never formed *de novo*, but it grows and increases ceaselessly; it is handed on from one generation to another like a long root creeping through the earth, from which at regular distances shoots grow up and become plants, the individuals of the successive generations'' (Vol. I, p. 416). ''This splitting up of the substance of the ovum into a somatic half, which directs the development of the individual, and a propagative half which reaches the germ cells and there remains inactive, and later gives rise to the succeeding generation, constitutes *the theory of the continuity of the germ plasm* (Vol. I, p. 411). According to this theory, the body or somatic cells serve only to protect, nourish and transport the germ cells which contain the germ plasm. Later the germ cells separate from the body and develop into new individuals and the body subsequently dies.

In the eggs of chrysomelid beetles the germ cells are formed at an extremely early period in embryonic development. They separate entirely from the embryo and come to lie in a group at the posterior end; at this time germ cells are quite distinct from somatic cells. Later the germ cells migrate back into the embryo, where they are protected, nourished and transported until they become mature, leave the body and give rise to a new generation.

What particular part of the germ cell represents the idioplasm or germ plasm? is a question of fundamental importance. Weismann recognizes the chromosomes as the germ plasm and has built up a complex theory as to the constituents of these bodies. The present discussion is not concerned in any way with the structure of the germ plasm as conceived by Weismann, and the writer does not wish to become involved in a consideration of idants, ids, determinants and biophores. The theory of dichromaticity (Dobell, '09) may aid in answering this

question. This theory holds that the chromatin of the germ cells is of two kinds—(1) idiochromatin, which is for reproductive purposes, and (2) trophochromatin which performs vegetative functions. In many Protozoa these two kinds of chromatin are separate throughout the life cycle. For example, in *Paramecium* the micronucleus is thought to represent the idiochromatin, the macronucleus, the trophochromatin (Calkins, '09). During conjugation and the subsequent reorganization of the nuclear apparatus the macronucleus breaks down and disappears, whereas the micronucleus gives rise not only to new bodies like itself, but also to new macronuclei.

In most animals idiochromatin and trophochromatin are supposed to be contained in one nucleus and are indistinguishable except in a few cases during the differentiation of the germ cells at an early developmental period of the egg. One is tempted to interpret as idiochromatin (1) that part of the chromosomes of *Ascaris* which is lost by the somatic cells (Fig. 1, *B*, *c*) but retained by the germ cells, (2) the nuclear material which is present in the primordial germ cell of *Cyclops* (Fig. 2, *B*, *ak*) but is absent from the somatic cells, (3) the similar substance in the primordial germ cells of *Oophthora* (Fig. 4, *n*), (4) the "besondere körper" in the egg of *Sagitta* (Fig. 3, *x*), and (5) the pole disc in the eggs of chrysomelid beetles (Fig. 5, *A*, *gc.d*).

One difference between these substances and the germ plasm as Weismann conceives it should be pointed out. In the cases cited above the material interpreted as germ plasm is only in one instance chromatin, and in this animal (*Ascaris*) it does not constitute the entire chromatin as Weismann's theory demands. If these extra nuclear bodies really represent the iodioplasm our location of the germ plasm must be transferred from the chromosomes to this material.

2. The second theory mentioned above, namely, that the extra material possessed by the germ cells determines these as such because of some fundamental principle of metabolism, seems more plausible than the theory just outlined. It is worthy of note that the primordial germ

cells of several animals belonging to widely separated groups are supplied with extra nutritive material. This is true in the Diptera, *Chironomus* (Weismann, '63) and *Simula* (Metschnikoff, '66), in the Lepidopteron, *Endromis* (Schwangart, '05), in the Elasmobranchs (Beard, '02), in the Teleosts (Eigenman, '92), in the Amphibia (Nussbaum, '80), and in the Reptilia (Allen, '06).

It has already been pointed out (Hegner, '09) that the pole disc granules may be nutritive material. "That the pole-cells need special means of nourishment is doubtless the case, for contrary to the condition in the blastoderm cells, they are at an early period entirely separated from the yolk, and later use up energy in their migration" (p. 275). If this is true, and as Wieman ('10) claims, the pole disc granules are derived from the yolk stream, our germ cell determinant hypothesis is not weakened, but gains a distinct argument in its favor.

It is interesting to note in this connection that two of the foremost investigators of the relation of the accessory chromosomes to sex determination are inclined to believe in the quantitative hypothesis, *i. e.*, that the egg which is fertilized by the spermatozoon containing the accessory develops into a female because there is more chromatin present, and that this plus amount influences the metabolism of the cell and its descendants (Wilson, '10; Morgan, '10). This hypothesis suggests the theory of sex advocated by Geddes and Thomson ('89), that "the female is the outcome and expression of preponderant anabolism, and in contrast the male of preponderant katabolism" (p. 132). In *Sagitta* (Elpatiewsky, '09), however, it is the male primordial germ cell and not the female that acquires the larger part of the "besondere körper."

Although neither of the two possibilities advanced in the foregoing pages may be correct, nevertheless it seems certain that the peculiar bodies in the primordial germ cells of the animals described above should be named "germ cell determinants." In any event, the attention of investigators ought to be directed toward the problem of discovering the origin and complete history of these

bodies, since their bearing upon theories of heredity is of fundamental importance.

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FURTHER OBSERVATIONS ON THE POSE OF THE SAUROPODOUS DINOSAURS

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SINCE the publication[1] of my paper on the manner of locomotion of the Sauropoda a number of communications have appeared which treat of the same subject. Two of these I wish especially to notice here, both of which have appeared in the AMERICAN NATURALIST, one of these being written by Dr. W. J. Holland;[2] the other by Dr. W. D. Matthew.[3] A third interesting and instructive paper, from the pen of Dr. O. Abel, appeared in March, 1910, in the *Abhandlungen der k. k. zool.-botan. Gesellsch. in Wien,* Volume V, Heft 3, pp. 1–60.

Dr. Holland experiences many difficulties in his attempts to articulate the bones of *Diplodocus* so as to give the animal a pose like that of the crocodile and of the lizard. His Fig. 9, on page 268 of his communication, is intended to illustrate some of his perplexities. "Of what earthly use," he says, "the hind limb of the *Diplodocus* could have been to him in such a position I leave you to determine for yourselves." Now, although the proximal ends of those femora are not all placed as they are in the lizard or the crocodile, nevertheless, taking them as Dr. Holland has placed them, it is difficult to see why, if they were not ankylosed with the pelvis and the animal had not contracted locomotor ataxia, it could not lift itself out of the hole provided for it. Furthermore, it is not necessary for lizards to carry their knees above the level of their backs; no more was it necessary for sauropods to do this. Dr. Holland finds trouble also at

[1] *Proc. Washington Acad. Sci.*, XII, 1910, pp. 1–25.

[2] AMER. NATURALIST, XLIV, pp. 259–283.

[3] AMER. NATURALIST, XLIV, pp. 547–560.

the knee-joint, when the leg is flexed, as shown in his Fig. 11, in which case, as he states, the tibia and the fibula come into contact with the condyles of the femur at two points not larger than as many sixpences. But we must suppose that the *Diplodocus* did sometimes lie down, and in so doing did bend its legs as much as Dr. Holland has represented, or more. Whoever has observed the effort required by a horse in regaining a standing posture can imagine the strain that would come on those femoral condyles and lower leg bones when the reptile endeavored to get on his feet again; but we can hardly suppose that the bones and cartilages of the knees were crushed every time the animal arose from its slumbers. Dr. Holland appears not to appreciate the fact that all these articular surfaces were invested with abundant cartilage.

Dr. Holland's Figs. 15 and 16 illustrate the embarrassments encountered by him in his efforts to adapt the bones of the fore leg to the positions that they have in the lizard. He would have had fewer difficulties had he not been laboring under the misapprehension that the upper end of the radius articulated with the inner condyle of the humerus instead of the outer. Such a transposition of the radius and ulna would present something unique in anatomy and, in the case of the sauropods, would be wholly unnecessary.

From the compressed form of the body of *Diplodocus* Dr. Holland has derived an argument against the proposition that the reptile had a creeping mode of locomotion. Dr. Abel also formulates the generalization that among the reptiles which in locomotion do not lift the belly and thorax from the ground but drag it, the cross-section of the thorax is transversely oval. It is true that most creeping animals have the body depressed, but they vary greatly with respect to the amount of depression. On the other hand, there are lizards which have the body strongly compressed and which nevertheless progress as do other lizards. A species of the genus *Gonyocepha-*

lus shown me by Dr. L. Stejneger has the thickness of the body only .57 of the height; so that it is nearly as much compressed as Dr. Holland has represented *Diplodocus* to be. Various other genera of lizards include species with much compressed bodies. Some of the tortoises belonging to the genus *Testudo* have the shell about twice as wide as high, while in *T. abingdonii*, from the Galapagos Islands the shell is fully as high as wide. Nevertheless, this tortoise shows no tendency to assume a mammalian gait. I see no reason why, if the necessities of the animal required it, the shell might not, in the course of time, become still higher.

It is of great value to have, from one so competent as Dr. W. D. Matthew, a statement regarding the value to be attached to the form of the femur in relation to the pose of the sauropods. Dr. Matthew seems to agree with me that straightness alone of the femur does not prove that these animals walked erect on either two or four legs, only, he appears to hold that the larger mammals and dinosaurs have in general straighter femora than their smaller and more agile ancestors. This statement is, of course, subject to the condition that the femur was not straight in the ancestors themselves. And when we come to apply the statement to the dinosaurs we are likely to dispute whether the femora of *Tyrannosaurus* are or are not less curved than those of some earlier dinosaurs. Dr. Matthew describes the hinder limb of the elephant and asserts that all gigantic mammals show some approach to this type; also, that in the sauropods the resemblance in form and proportion of the hinder limb to that of the elephant is very marked. However, a number of the genera that he mentions as illustrating his views seem to me not to conform well to the specifications. *Titanotherium* does not, if we may rely on the restorations,[4] have post-like legs nor, in comparison with the elephant, short feet. *Coryphodon* does not have straight legs,[5] nor is it a gigantic mammal, being ex-

[4] *Bull. Amer. Mus. Nat. Hist.*, VII, pls. VIII, X, XI.

[5] *Bull. Amer. Mus. Nat. Hist.*, X, pl. X.

ceeded in size by some of the rhinoceroses, which again have very angulated legs. It is to be noted, too, that most of the genera mentioned by Dr. Matthew as being gigantic mammals of diverse stocks are extinct, and there might be some differences of opinion as to the exact form of their legs and even of the feet.

Nor is it certain that the type of limb found in the elephant is the result of the great size of the animal. The limb has probably not changed greatly since Middle Eocene times, when elephants were small animals; although its angulation has probably become somewhat reduced, the femur relatively somewhat longer, and the digits a little shorter. The femur of *Mœritherium*, supposed to be a relative or even an ancestor of the elephants, from the Middle Eocene of Egypt, is only eleven inches long and is as straight as that of the living elephant. The type of leg possessed by the elephant is rather primitive in its structure and is found in such animals as are slow of movement. All animals have some means of protecting themselves more or less effectively from their enemies. Horses, deer and oxen have developed angulated limbs, with short humeri and femora and elongated metapodials, combinations that confer the power of rapid flight. The elephants have found their safety in their great size; and extensive modifications of their legs have not been required.

As is well known, the lizards have straight-shafted femora, which are longer than the tibiæ, and the digits are long. As, however, the land tortoises may have short digitigrade feet, it is difficult to see why some lizards might not develop such feet. And it is not improbable that such a lizard might attain a great size and continue to retain its straight femora, short feet, and angulated limbs.

In short, it seems to the writer that Dr. Matthew's proposition as regards the significance of the straight femur is loaded with so many conditions and subject to so many exceptions, known and supposable, that it must

be applied with great circumspection to the dinosaurs.

It is frequently asserted that the pelvis and the limbs of the diplodocus possessed analogous resemblances to those of the elephant. In the pelvis these are confined, I believe, to the great size and to the convex iliac crest. In the sauropod the ilia are directed from front backward; in the elephant almost transversely. The pubes and ischia in the two animals are utterly different. The acetabula are different in form, size and position. The femora of the two animals are alike large and straight-shafted. That of the sauropod, however, has no great trochanterial process; and whether, as my critics contend, only the inner angle of the proximal end of the femur or, as I insist, the whole of the proximal end, is to be regarded as the head of the bone, this head is very different from that of the elephant. The size of the radius relatively to the ulna and of the fibula to the tibia is very different in the two animals. The digits of the elephant, in general, are far less reduced than those of the sauropod. That the limbs of the sauropods were straight like those of the elephant has been assumed; but we are now discussing that proposition.

On the outer border of the upper end of the femur of *Diplodocus* is a rugose area which extends downward a distance equal to one fifth the length of the bone, perhaps somewhat more. This, or at least its lower end, represents the trochanter major. According to Dr. v. Huene's figures, this trochanter occupied about the same level in the Triassic dinosaurs, but it was placed somewhat more on the dorsal surface of the bone. Osborn[6] represents this trochanter in approximately its correct position, but not extended far enough downward, as is evident from the photograph reproduced on his Plate XXIV. Dr. Matthew speaks of this trochanter as a "clearly marked rugosity around the proximal external angle of the head." I find this rugose surface on other sauropod femora. The upper half of a large femur in

[6] *Mem. Amer. Mus. Nat. Hist.*, I, p. 210, Fig. 14.

the U. S. National Museum measures 510 mm. across the bone just below the rough proximal end. On the fibular border the rugose surface that represents the great trochanter runs down on the bone a distance of 390 mm. At this point there is a decided angle in the border on the bone. A rough surface just like this in position and extent is found on the femur of the crocodile.

This being settled, we may turn our attention to what Marsh and Hatcher called the great trochanter, the outer half, or nearly as much, of the rough proximal end of the femur. Those who do not believe that this formed a part of the head of the bone and was not inserted in the acetabulum ought to explain what it represents.

As regards the distal end of the femur of *Diplodocus*, I do not see in what way it is essentially different from that of the lizard. Dr. Matthew says that in the latter the distal articulation for the tibia and the fibula are on the back of the femur, not on its end. As I see the femur of *Diplodocus* and that of the lizard, both have a broad articular surface on the end; and this surface is continued around on the ventral side of the bone, being there divided into two parts by the intercondylar fossa. It must not be supposed that I see no differences among the femora of the diplodocus, the crocodile and the lizard; but these are much nearer one another than that the diplodocus is to the femur of the elephant.

Dr. Holland has made the objection that in articulating the leg bones of *Diplodocus* so that there might be a right angle between the femur and the tibia there would be no surface against which the end of the femur might articulate. However, the same condition would exist in the flexed knee of the horse or of man were it not for the patella. In the flexed knee of the lizard and of the crocodile the end of the bone is covered by the tendon of the extensor muscle and the ligaments; and certainly the same was true in the sauropods. On account of the deep body of *Diplodocus* it would not probably often happen that the angle between the femur and the tibia

would be less than a right angle. When the leg was extended forward it would be nearly straight and again straight when directed backward. Also, the body would be lifted somewhat. It is an erroneous idea, held apparently by both Dr. Matthew and Dr. v. Huene, that in walking the crocodiles, lizards and turtles do not lift the body from the ground. Probably all do so; even the gigantic Galapagos tortoises carry their bodies free from the ground.

Inasmuch as the arrangement of the bones of the fore leg has been brought into this discussion, I shall make a few remarks on the subject. Few of the figures of the humerus give a correct notion of its form. Those published by Osborn and Granger[7] show well the characters of the bone, seen from the front only, in three genera of sauropods. A humerus in the U. S. National Museum, supposed to be that of *Diplodocus*, has the proximal border broad and convex and very rough, showing that it was covered by cartilage and doubtless formed a continuous articular surface. This surface played in the glenoid fossa or notch of the shoulder girdle. About the middle of this convex surface the bone is much thicker than at the ends and the thickening is on the dorsal face of the bone. This thickened portion quite certainly corresponds to a rounded elevation seen on the upper surface of the proximal end of the humerus of the crocodile, and this in its turn is probably homologous with the more narrowly limited head of the humerus in mammals. In the crocodile this elevation fits well into a depression in the scapula, in the roof of the glenoid fossa. When, however, the leg is brought well forward the elevation slips out of the glenoid notch and a part of the head farther forward takes its place and supports the weight. I believe that the same movements took place in *Diplodocus*.

Now, in the restoration of *Diplodocus* in Pittsburgh and in that of *Brontosaurus* in New York, the humerus is placed in the glenoid notch in an approximately verti-

[7] *Bull. Amer. Mus. Nat. Hist.*, XIV, p. 203.

cal position, with the deltoid border directed outward. the opposite border inward, and the primitively dorsal surface directed forward. This leaves the inner, probably lesser, tuberosity projecting far within the inner surface of the shoulder girdle. An examination of a lot of mounted skeletons will show that in all mammals that walk by moving the limbs in sagittal planes the inner tuberosity is greatly reduced and removed to a position in front of the head of the bone, and little or none of the humerus projects beyond the inner surface of the scapula. In two mammals I find a large process which corresponds, in position at least, to the inner one of the sauropods. These are the echidna and the duck-bill, and both of these mammals move the legs as the creeping reptiles do. I believe that the prevailing manner of articulating the humerus of the sauropods is wrong. It ought to be placed in a plane approximately horizontal, with the lower and upper faces in their primitive positions, with the deltoid border forward, and, when the leg is in a median position of its swing, with the thickening of the proximal articulatory surface in contact with that part of the glenoid notch that is formed by the great ridge that passes across the scapula. In case the leg is placed further forward or further backward, corresponding parts of the convex articular end of the humerus ought to pass under this ridge. There was no need at any time of life that the lesser tuberosity should project against the ribs or into the muscles. The arrangement that I have described is that which may be observed in the crocodile also.

If now the ulna and the radius are articulated properly with the humerus the whole leg will function as it does in the lizard and the crocodile. In the U. S. National Museum is a specimen, shown me by Mr. Chas. W. Gilmore, which consists of the radius and the ulna, somewhat crushed, but preserving nearly their original relations to each other. These bones differ somewhat from those of the crocodile, as might be expected. The

principal difference is found in the fact that the upper end of the ulna extended across the lower end of the humerus and has a concavity in front for the head of the radius. The ulna and radius appear to have been more closely bound together at the lower ends than in the crocodile; nevertheless, the bones of the two reptiles resemble one another closely. When to those of the sauropod a humerus of corresponding size is fitted, with the outer (anterior) condyle in contact with the head of the radius, the leg is strikingly like that of the crocodile. In my opinion, Marsh's arrangement of the bones of the fore leg of *Brontosaurus*[8] is more nearly correct than later restorations of this limb in the same animal and in *Diplodocus*. In the figures referred to, the humerus, in the middle of the step, presents the dorsal surface outward; whereas, in the Pittsburgh and New York restorations this surface looks backwards and the deltoid border looks outward. If Marsh's figure were modified so that the humerus were horizontal or nearly so, the leg would have nearly its natural position.

Various opinions are held regarding the question whether the sauropods were strictly aquatic, strictly terrestrial or amphibious. In my paper published in the *Proceedings of the Washington Academy of Science* I called attention to a figure that illustrates Cope's views and to another published by Matthew that elucidated Osborn's ideas. Dr. Matthew's views seem to differ from those of Osborn in that the former maintains that these reptiles usually preferred not to be wholly submerged and that they could not leave the water without endangering the integrity of their limbs. He finds his reasons for his opinion as to the depth of the water preferred in the fact that the bones above a line drawn from the hip joint to the shoulder blade are of light construction, while those below this line are thick and heavy. This line is his "water-line" and indicates the average depth of the water haunted by these reptiles. The heavy

[8] The Dinosaurs of North America, Pl. XLII.

bones of the legs were intended, according to Dr. Matthew, to hold the animal down in the water, as the lead in the diver's shoes holds him on the bottom. However, it occurs to the present writer that if the sauropods were accustomed to wade in water that came only a little more than halfway to their backs the weight of the unsubmerged part of the body would suffice to hold them to the bottom. A man who wades in water only waist-deep does not need leaden soles. To maintain the theory, it seems necessary to keep the reptiles more deeply submerged. To do this it is only necessary to suppose that they crawled about at the bottom of the water as crocodiles do. If we suppose that the sauropods walked wholly submerged and erect on four legs the differentiation observed by Dr. Matthew in the ossification might be explained on the supposition that it was for the purpose of ballasting the animals. However, it does not appear that the hippopotamus, an eminent wader, needs to be steadied in this way. Furthermore, why should it have disturbed such facile swimmers as the sauropods probably were to heel over occasionally?

Notwithstanding the means employed by nature to reduce as much as possible the weight of the skeleton, the bodies of the sauropods were very heavy. The bones of the legs were well-developed and I recognize that they were not as hollow as those of a horse, for example. Can we not, after all, most reasonably explain the case by supposing that the sauropods went about more or less on land and needed strong legs to hold up their heavy bodies?

In my former article I expressed the opinion that it was hardly possible for a diplodocus to walk about wholly submerged. It appears that Cope and Osborn and Matthew have thought that the animal would have no difficulty in doing this. Perhaps the question can never be definitely decided. The hippopotamus is said to walk beneath the water and probably does really do so; at least they remain for considerable periods be-

neath the water and move about. They are active swimmers and it is possible that their movements along the bed of the river or lake are to a considerable extent due to the action of their feet against the water. They have massive skeletons which have evidently been developed to bear them down in the water. Nevertheless, it is to be questioned whether the animal exerts any considerable pressure on the bottom. If the specific gravity were any considerable amount above that of the water the animal would have difficulty in coming to the surface for air and to get a view of its surroundings. Tapirs too are said to be great swimmers and divers and to run along on the bottoms of streams; but these mammals have no special modifications of the skeleton to enable them to do this. Possibly they lay hold of the bottom in some way with their hoofs, or, while running they may incline the head and body downwards and forwards, like a descending aeroplane. That the hippopotamus with his heavy skeleton has a specific gravity little above the water is proved by the following fact related in Brehm's Thierleben: When a hippopotamus is killed he at once goes to the bottom. Nevertheless, in many cases the body comes to the surface within from 30 to 60 minutes, a result of the development of gases within the cadaver. Hence, it is extremely doubtful whether the animal can exert much pressure on the bed of the stream. So too, even if the sauropods did walk about at the bottoms of streams, wholly submerged, they must have rested there very lightly.

Now what conclusions can we draw from the facts above established? Dr. Matthew's strongest argument in favor of the erect pose of the sauropods is derived from the supposed resemblance of their limbs to those of the elephant, the long straight femur, the short digitigrade feet, and the slight angulation of the limb. "Obviously," says he, in describing rectigradism, "a specialization of this kind will occur only in an animal which habitually rests its weight on the limbs." But we are

dealing here with animals that are supposed to have the whole, or at least nearly the whole, of the weight taken from their limbs.

Moreover, does not the one part of Dr. Matthew's theory contradict the other? He has told us that the parts of the skeleton below the water-line were heavy for the purpose of overcoming the buoyant effect of the water, as the lead in the diver's shoes does. Then, as shown in the preceding paragraph, he maintains that there was pressure enough to produce such legs as the elephant has, an animal whose legs must support its whole weight.

We may now be permitted to inquire whether or not aquatic life is likely to have produced either of the effects attributed to it by Dr. Matthew. The hippopotamus is an animal far less aquatic than Cope and Osborn and Matthew have supposed the sauropods to have been. Its limbs are almost ridiculously short, so short that when it is quitting or entering the water its belly leaves broad and deep channels in the mud through which it wades. The leg bones are indeed very strong, a result conditioned by the frequent excursions made on the land. The feet are the most primitive possessed by any living artiodactyl, and the digits are bound together by a short web. The aquatic performances of the tapir have not contributed to its structural uplift, for its feet are among the most primitive of those of the perissodactyls. Let one only view with some attention a series of mounted skeletons and one will soon be struck with the fact that degenerative changes begin to affect the limbs of animals very shortly after they begin to confide to the water the support of their bodies; and these degenerative modifications continue to manifest themselves until the limbs have been converted into paddles and flippers or reduced to vestiges or even extirpated.

That the sauropods had originally been amphibious and then became strictly aquatic seems to the writer highly improbable. Those short digitigrade feet, with

toes having a reduced number of phalanges, seem to furnish almost positive proof that their possessors had for many generations been accustomed to travel on solid ground. It is probable that their resort to the water had not endured long enough yet to affect to any great degree their organization, except as to size.

Dr. Matthew believes that at some stage the ancestors of the sauropods were bipedal and that later they became secondarily quadrupedal. He grants that the indications of former bipedalism in this group are less apparent than in the quadrupedal Predentata. It is easy to agree with the latter opinion. As to the hinder limbs, we ought to expect that bipedal locomotion would have led to the development of smooth, well-finished articular surfaces and of a trochanter major standing out as a distinct process near the upper end of the femur. Why, on the resumption of quadrupedal locomotion, should these acquisitions have disappeared as if they had never existed? This has not happened even in the walruses, seals, porpoises and manatees, which forsaking the land, have betaken themselves to the water. The inevitable result, if not the prerequisite, of bipedalism is a considerable reduction in the size of the fore legs and various transformations of the hands. But the fore limbs of *Diplodocus* and of *Brontosaurus* show no reduction in size. Are we to suppose too that while the fore legs were held from contact with the ground and were probably employed for other purposes than locomotion, they continued to progress in digitigrady? Those fore feet look as if they had been walked on fully as much as the hinder feet.

From a photograph of the fore foot of a *Diplodocus* in the American Museum of Natural History Dr. v. Huene concludes that this foot was exaxonic. It would be interesting to learn more about this foot, especially whether or not the bones were found in their natural relations. The foot differs from that of some other sauropods, certainly. With the ulna and radius before

mentioned, in the U. S. National Museum, there are present all the metacarpals and some of the phalanges. Through pressure two of the metacarpals, the fourth and the fifth, have had their hinder faces squeezed against the hinder faces of the other three. Otherwise, the bones retain their original relationships. Of these the first is distinctly larger than the fifth. The lower end is especially enlarged, to support the phalanx and the great claw. It is proper here to say that Dr. v. Huene has very justly criticized the representation of the feet of *Diplodocus* as presented in my plate published in the *Proceedings of the Washington Academy of Science.*

Dr. Matthew refuses to accept my explanation of the tracks made by the supposed iguanodon. Those tracks are certainly in need of explanation. So far as I am aware, no one has as yet ventured to mount a dinosaur with the toes pointing inward after the manner of those tracks.

Neither does our author accept my suggestion that some of the tracks found in the Triassic sandstones of the Connecticut River Valley were made by birds. The conclusion appears to be that, because a few dinosaur *bones* have been found in that region, therefore all the *tracks* are those of dinosaurs. Dr. Matthew does not attempt to show how animals built as were the Triassic dinosaurs that we know, with short diverging femora, rather short lower leg bones, and short metatarsals, could put one foot directly before the other in walking or running. It is much to be doubted whether a running duck or penguin could do this. And are we to suppose too that those Triassic dinosaurs were always running? It may be easy in mounting the skeleton of a dinosaur to place the femora parallel or even to bring the knees together. In life the thighs could not take this position, unless on each side there had been a considerable excavation at the junction of the ponderous belly and the thick tail, a sort of little wheel-house for the thigh to

play in. It seems quite doubtful whether the carnivorous dinosaurs of even the Jurassic period had the erect bird-like bearing that is usually attributed to them. The extraordinary development of the pubic bones of *Ceratosaurus*, whose expanded and ankylosed distal ends reached nearly half-way to the fore legs, seems to me to indicate that these animals, when in repose, had a prone position, resting much of the weight on the pubes, and that when running their legs straddled considerably.

Dr. Matthew thinks that the sauropods had too great a bulk to have lived on land. The law to which he gives expression does, of course, prescribe a limit to the size an animal can attain, but who has yet determined what that limit is? Larger elephants have lived than those now living, and it is not certain that we have discovered yet the largest that have lived. Animals do not attain a great size simply to test the laws of mechanics.

SHORTER ARTICLES AND CORRESPONDENCE

COMPUTATION OF THE COEFFICIENT OF CORRELATION

In Dr. Harris's recent note[1] suggesting a helpful modification of the method of computing the coefficient of correlation, the only objection mentioned is the fact that his method results in very large product-numbers. This difficulty can be considerably reduced by a procedure based on the fact that the calculation of the standard deviation and the coefficient of correlation does not depend upon the absolute dimensions of the things measured. All that is required is a given series of successive grades; the standard deviation will then be obtained in terms of the units separating the grades, whatever they are; while the coefficient of correlation is a relative number, quite independent of the value of the units. We may therefore give to the lowest grade of both sets of measurements (x and y) the value 0, for the succeeding ones the values 1, 2, 3, 4, etc., instead of the real values; the labor of computation will then be greatly reduced, while the same value will be found for the two constants in question. The values which Dr. Harris calls A_x and A_y will by this method not be the means of x and y (so that they may well be designated rather d_x and d_y), but the means can be obtained from them without labor by simply adding to each the absolute value of the lowest grade of x and of y, respectively (since we had reduced all grades by this amount, in substituting 0 for the lowest grade).

This much simplifies the computations when the absolute dimensions are represented by numbers considerably greater than unity. Thus, in Dr. Harris's Table III., in finding the standard deviation we should for the third grade have to multiply by but 4, instead of by the square of 28.

H. S. Jennings

NOTE ON BATRACHOSEPS ATTENUATUS ESCH.

Batrachoseps attenuatus is the most abundant salamander in the vicinity of Stanford University. During the rainy season

[1] This journal, November, 1910.

it can be found under nearly every rock and log on the neighboring foothills. No one has, so far as I am aware, discovered and described its egg-laying habits. The author obtained some of the eggs of this salamander and the following brief note is published with the hope that it may attract the attention of some student to this problem.

The first eggs obtained were discovered by T. Kimura during January, 1906. They were found partly buried in depressions under rocks on a moist hill side. On January 5, 1907, the author found some eggs under a log in a moist ravine well up in the hills. The eggs were deposited in small pockets in the ground; 21 were in one group and 10 in another group about 2 feet distant, while 4 were scattered between, suggesting that all were deposited by a single female. These eggs were round or slightly oval and about 6 mm. in diameter. Development was well advanced. The first individual to issue from the egg appeared on January 28, and was 17 mm. in length and of a dull black color. By May 22 it had doubled in length and was 35 mm. long. The majority of the eggs, when found, were covered with a fungus and failed to develop. This suggests that they may have been under abnormal conditions. It seems very likely that the majority of the eggs of this species are deposited just beneath the surface of the ground, as is the case with earthworm eggs and so escape detection. Diligent search at the proper season should settle this question.

Batrachoseps attenuatus disappears from this region with the approach of the dry season and appears suddenly in the fall after the first heavy rains. I have been informed that it can be obtained at any season in the moist coast region near Pacific Grove. It seems probable that in the dry regions this salamander burrows into the ground as the earthworm does to escape the drought. This theory is supported by the shape of the body, which is elongate, slender and roundish, suggesting that of the earthworm. It appears that we have here a parallel development of form and habit between *B. attenuatus* and the earthworm due to a struggle against the same physical environment.

C. V. BURKE.

NOTES AND LITERATURE

SOME RECENT STUDIES ON VARIATION AND CORRELATION IN AGRICULTURAL PLANTS

From the nature of his material the student of agricultural problems has an unexcelled opportunity to collect large masses of statistical data. Domestic animals and plants, particularly the latter, can be easily propagated in vast numbers under conditions controlled in all sorts of ways. Not only the opportunity, but also the desirability, of collecting data on a statistical scale, has been recognized by agricultural investigators from the beginning of experiment-station work in Germany, and still earlier by individual students in this field. Much of the early statistical material relating to agricultural objects or problems still remains unanalyzed and undigested, because of a lack of adequate statistical methods, on the one hand, and a lack of acquaintance on the part of the collector of the data with what mathematical methods did exist for the analysis of such material, on the other hand.

It was obviously to be expected that a system of adequate biometric methods, such as that which has been developed by Professor Karl Pearson, would in due time come to play a conspicuous part in agricultural investigations. This time is coming. One who follows the current literature of agricultural science, in a broad sense of the term, can not fail to be struck with the rapidly increasing use of these mathematico-statistical methods during the last few years. In so far as the methods are correctly and appropriately used this is a most commendable movement. But it must always be kept in mind not to let admiration for the method *per se* blind one as to the real significance and importance of the biological problem attacked. The futility of dealing biometrically with data or problems which lack a sound biological basis is obvious. The indiscriminate application of biometric methods to all kinds of data is easily seen upon critical examination, to have only so much value or validity as resides in the original data themselves. It is particularly important that this point be kept in mind in agricultural work along biometric lines, because of the great ease with which mere statistics can be collected in this field, and the consequent temptation to collect them without critical consideration of their meaning and worth.

It is the purpose of the present review to discuss some of the recent work which has been done along biometric lines with agricultural materials and on problems relating to the science of agriculture. The list of literature at the end or the review based on it does not aim at completeness either in respect to the period or the field covered. Rather it is the aim to indicate the general trend of work in this field and to discuss its points of strength and of weakness.

At the outstart should be mentioned a number of papers which have dealt with the general subject of statistical methods as applied to agricultural material. The general purpose of such papers has been, on the one hand, to call the attention of agricultural workers to the existence of such methods and to the desirability of their use, and, on the other hand, to give some account of the nature of the methods themselves. Here are to be noted the papers of Albrecht, Roemer (introductory portion), Schoute, Quante, Rietz and Smith, and Zaleskiego. The last three papers are especially worthy of attention. The paper of Rietz and Smith gives an excellent elementary discussion of correlation. It further furnishes a most hopeful sign of the rapid development in research standards in agricultural work in this country. Zaleskiego makes keen analytical use of frequency polygons in his breeding work. He calls special attention to the prime importance of not lumping together non-homogeneous material. Rather he urges studying the frequency polygon derived from the progeny of each "pure line" by itself. Then later these separate polygons may, if there is reason for it, be summed together to make a "general population" polygon. But to start with the latter and neglect the biological units (pure lines) which go to make it up is wrong. This insistence on the strict biological or gametic homogeneity of material to be studied by statistical methods is worthy of all commendation.

Quante discusses from a general standpoint some of the problems of variation in agricultural plants. He considers that a definite morphological difference is certainly present between species, varieties or groups when their means differ by five or more times the probable error. He shows that in a number of characters of barley and wheat which he studied the variation is distinctly skew. In a selected strain of rye he found clear evidence of a "normal" or Gaussian symmetrical distribution of variation.

Turning our attention next to special investigations we may

consider different crops separately and take wheat first. Here the studies of Roberts and his students take a leading position. For some years this investigator has been engaged upon a very comprehensive biometrical study of wheat. Only fragments of this work have as yet been published. We may first consider his paper on "A Quantitative Method for the Determination of Hardness in Wheat." An apparatus was devised by which the weight in grams necessary to crush a grain of wheat could be directly determined. The problem was to find out how large a random sample of kernels must be taken in order to reach a reliable result as to mean crushing weight for a variety or strain. Samples of from 100 to 500 kernels each were tested and the mean for each sample determined, two varieties of wheat —a hard and a soft—being used. It is shown that the mean crushing weight diminishes regularly and rapidly as the size of the samples increases, until a minimum at a sample of 450 kernels is reached. Samples of 500 kernels show an increase in mean crushing weight over the 450 kernel sample. Why the *mean* crushing weight should regularly diminish with increasing size of sample is not clear, and is neither explained nor even discussed in the paper. That the *error* of the mean crushing point would diminish with increasing size of sample is obvious. The error of the mean is found, as a matter of fact, to diminish according to a hyperbolic curve. A mathematical discussion of this curve of the errors of the means is given, and examination of the second differential shows that the *rate* of diminution of the error becomes negligible after a sample or group size of 350 kernels. It is then concluded that 350 kernels is a sufficiently large sample to use practically in determining mean crushing points.

Roberts's paper on "Breeding for Type of Kernel in Wheat" is a very thorough and extensive biometrical study of the form of the wheat kernel in many different pure lines or races. Means only are given in this paper, but the amount of measuring and computing involved must have been literally stupendous. Only such a biometrical organization as that maintained at the Kansas Station could have managed it. Data are given on mean length, width, length/width index, volume, weight, and specific gravity of the individual kernel, samples of 500 kernels being taken in 5 separate 100-kernel lots for each pedigree strain (pure line). Also determinations were made of the weight of 100 c.c. of grain, of a packed and a struck bushel of grain, and of the percentage volume not occupied by grain when a 100 c.c. measure is filled

with grain. This last determination was made by the alcohol method. The upshot of this elaborate study is to show that the *shape* of the grains as measured by the length/width index is a very significant factor in determining how wheat will grade according to commercial standards. It is shown that "a difference of at least as high as three pounds per bushel may exist between different pure-bred wheats having identical average kernel-volume and kernel-weight." The final conclusion is that the percentage volume of grain in a packed measure would be a much more just and scientific basis for market grain grading than the present system of test bushel weight. This paper illustrates in a very striking way how the scientific method can solve in a precise and final manner a practical commercial problem.

Lill has made a quantitative study of the relation of size, weight and desirability of kernel to germination in wheat. His data indicate that germination capacity is not correlated with size of kernel, but is correlated with density of kernel. No biometrical analysis of the data is attempted.

Waldron has made an interesting and significant biometrical study of the correlation between weight of grain and other plant characters in oats and wheat, using his own measurements for the former cereal, and published data for the latter. He shows that in oats the mean grain weight per head is *negatively* correlated to a rather high degree with (*a*) number of grains per head, (*b*) length of head and (*c*) length of culm. This obviously leads to a somewhat paradoxical result, namely, that when plump, heavy seed is sown, it is seed which is taken from mother plants which are *below* the average in size and yield. Yet careful experiments, covering a period of years, have shown that planting heavy seed gives increased yields. In other words, a practise which amounts to continued selection of the *poorer* yielding of plants as parents results in *increased* yield in the progeny. This paradoxical result needs analysis by careful pedigree breeding.

Clark has published a general biometrical study on variation and correlation in timothy, the material being gained in connection with the extensive breeding experiments with this grass which have been in progress for some years at Cornell University. The point of chief interest and novelty in the work is that each of the 3,505 plants which furnished the data was under observation during three consecutive years. The material thus gives some basis for an estimation of the relative influence, on the one

hand, of germ-plasm (*i. e.*, germinal determinant factors of whatever sort), which presumably was identical for each plant during the three years, and environmental factors, on the other hand, in determining observed degrees and kinds of variation in the adult organism. The results taken as a whole show that what might be called the general variation *facies* of a population of *Phleum* must depend to a very high degree upon "nurture" rather than "nature." The degree of variation, the degree of skewness of the variation curves, the closeness of correlation between different characters of the plant—all these are changed by general environmental conditions to a marked extent. Thus to take an example: the coefficient of correlation between weight and height of plant is given as .274 ± .011 in 1905 and as .718 in 1907. This is a *relative* change of nearly 200 per cent. In another case a significant positive correlation one year becomes significantly negative two years later. In general the heights (or weights) of timothy plants in any one year are correlated with the heights (or weights) of the same identical plants in another year only to about the degree indicated by a coefficient of around .5, which is but 50 per cent. of perfect correlation.[1] In other words, it appears on the basis of this result that in determining what a given timothy plant shall be like next year in respect to such characters as height and weight the innate constitutional, hereditary factors within the plant are on the whole of neither greater nor less importance than external environmental circumstances. In this case, and in respect to the characters dealt with, "nature" and "nurture" are about evenly balanced, with what advantage there is on the side of "nurture." The author emphasizes the practical significance of a result of this kind to the man who is carrying on selective breeding, and who obviously must make his selections at the outstart on the basis of the visible somatic characters as they are developed at the particular place and time at which he is doing his selecting. The paper is unfortunately marred by arithmetic errors.

It is a well-known fact that European workers (other than English), generally speaking, have very little acquaintance with biometric technique. A good example of this fact is afforded by a paper of Grabner on the problem of correlated variation in barley. The investigator desired to learn what relation existed between the economically valuable characters of this cereal. He collected a vast lot of statistical data regarding such characters

[1] Cf. Clark's Table VIII.

as yield of grain, hectoliter weight, weight of 1,000 kernels, size of kernel, protein content and "mealiness" or softness of grain. Instead of proceeding by the straightforward method of forming a correlation table and deducing therefrom the coefficient of correlation the author follows the laborious, inaccurate and inconclusive plan of averages. Virtually what is done is to calculate the observed regression line of one character on another. The general result reached, though in no wise critically supported by the evidence presented, is that all of the purely physical characters are correlated together to a high degree. The chemical and chemico-physical characters protein content and "mealiness" are not demonstrably (by the method used) correlated with other characters, though they are mutually definitely correlated. The chief scientific value of the paper is to illustrate in a striking manner how crude and clumsy were pre-Galtonian methods of attacking a simple statistical problem.

Turning now to corn, we have a number of studies of a more or less biometrical character. Apart from the primarily genetic studies on maize of East, Shull, Collins, and Pearl and Surface which are quantitative in character and to some extent[2] biometric in the treatment of the data, there have appeared recently two special studies on variation and correlation in this plant. The first of these is the paper of Rietz and Smith and the second that of Ewing. The objects of the two papers are apparently somewhat dissimilar. Ewing's is primarily a biological investigation, whereas Rietz and Smith apparently desire primarily to set forth the method of measuring correlation, and incidently to illustrate these principles by means of some corn data which they have on hand. The only general result of particular biological significance brought out in the work of Rietz and Smith is that the degree of correlation between various ear characters (length, circumference, number of rows, weight) is very markedly influenced by environmental conditions surrounding the growing crop. This paper is to be commended for its clear exposition of the method of calculating a correlation coefficient.

Ewing's paper contains more matter of general biological interest. Especially to be mentioned is the valuable discussion of the literature of correlation. The general problem which formed the basis of this investigation was to learn in how far the

[2] Shull gives some very interesting data in the form of variation constants (mean, standard deviation, and coefficient of variation) for variation in number of rows on ear in pure and cross-bred (F_1 and F_2) maize.

determination of statistical correlations between different parts of the maize plant might be of use to the practical breeder. The general conclusion to which the author comes in regard to this point is as follows:

Considerable study of the subject has forced upon the writer the belief that it is improbable that much use can be made of correlation in practical breeding. There are rare cases in which the coupling of unit characters may aid the breeder in making selections at an early period, but the existence of correlation in the fluctuating variability of two different characters is not likely to prove of much assistance. Nothing more than a moderate degree of correlation is likely to be found in these cases, unless some such relation as cause and effect exists between them. This is especially true of correlation between seed production and other characters, since the former depends upon a large number of other characters and conditions.

The correlations studied were those of weight of grain per plant (measuring *yield*) with each of the following characters: (1) Diameter of stalk, (2) length of leaf, (3) breadth of leaf, (4) height of mature plant, (5) height of seedling, (6) number of internodes, (7) average length of internodes, (8) percentage of internodes below the ear, (9) length of ear at appearance of silks, (10) date of appearance of tassel, (11) date of appearance of pollen, (12) date of appearance of silks, (13) duration of flowering period (pistillate flowers) in days, (14) number of branches in the tassel.

The coefficient for correlations 1–6, inclusive, 9, 10 and 12, are, in each case, from 5 to 19 times the respective probable errors. They are thus statistically significant. In view of this fact the statement in the general discussion of results that "in most cases the coefficient of correlation is so small that it is probably not worth while to try to classify it or even to conclude that there is correlation," seems not to have been very well considered. The same criticism is to be made against the paper of Clark discussed above. These authors appear to overlook the fact that whether a correlation is statistically significant (*i. e.*, whether correlation "*exists*") depends not upon its absolute value, but upon its relation to its probable error. A coefficient of $.0009 \pm .0001$ would be to a high degree of probability *statistically* significant, though absolutely small.

The garden pea (*Pisum sativum*) has been the subject of several recent biometric studies. At the Massachusetts Station Waugh and Shaw have been for some time engaged in an

investigation of inheritance in this form, conducted along biometric lines. In their first paper here reviewed they present variation data regarding the four following characters: length of vine, number of pods per vine, length of pod, number of peas per pod, and total peas. The raw data are not given and the discussion is very meager. Graphs of the variation curves are given, but instead of making these plottings of the actual frequency data as polygons, the authors connect the plotted points by free-hand sweeping curves. This is certainly a simple and expeditious, if somewhat naïve, method of curve-fitting! It is much to be regretted that such an inadequate, and indeed absolutely incorrect, method of presentation of statistical results should have been resorted to. In the discussion of heredity stress is laid upon the varying degrees of prepotency observed in the transmission of characters by individual plants. To measure this a new "coefficient of heredity" is proposed. The formula for this is

$$C = 1/\sigma D,$$

where C is the proposed coefficient, σ the standard deviation of offspring and D the difference between the parental character and offspring mean of the same character. It is obvious that the more nearly the offspring are like each other, and like the parent the larger will C become. It is somewhat unfortunate that this is called a "coefficient of heredity," since this term is in common biometrical usage for a very different constant. Indeed, in their own paper Waugh and Shaw use this term not only for their proposed constant, but also for the correlation coefficient between parent and offspring. A satisfactory measure of *individual* (not *average*) prepotency is a thing which is badly needed in breeding work. While the constant C proposed by Waugh and Shaw meets some of the conditions which such a measure must fulfill, it unfortunately appears to be of rather restricted significance and usefulness. The numerical value which it takes for different characters are not comparable one with another. The reason, obviously, is because the numerical value will change in accordance with the absolute rather than the relative variability of the character. An elephant and a mouse each equally prepotent with reference to the transmission of any character, say skull breadth, would have very different values of C for this character. Further, the constant becomes rather difficult to manage in cases of biparental inheritance, or

in those cases of undoubted prepotency, which are of the greatest interest and importance both theoretically and practically, wherein the prepotent individual does not itself have the character with regard to which it is prepotent expressed in its own soma. An example here is the dairy bull, prepotent in respect to milking qualities.

A continuation of this work on peas is reported in the second paper by the same authors. Data are presented showing the relation between observed variability and environmental (seasonal) conditions. The interesting point is brought out that there is less variation, and a higher correlation between parent and offspring, in respect to vine length, than in respect to either number of pods per vine or total peas per vine.

Roemer gives a very detailed biometrical study of pure lines in peas. The work is essentially a confirmation, with another plant, of Johannsen's epoch-making investigations on beans, though it lacks any extensive studies on the effect of selection within the pure line. The essential objective point of Roemer's research is rather to determine the biometric characteristics of pure lines as such in relation to the general population. Among the more important general results are the following:

1. The different biotypes in a population arrange themselves in frequency distributions in accord with Quetelet's law.

2. No relation was found to exist between the variability of the biotypes (*i. e.*, variation within the general population) and variation within the pure lines.

Shaw has made a very thorough biometric study of variation in the Ben Davis variety of apples and presents a mass of data of considerable general biological interest. When one recalls that commercial apple varieties are propagated by vegetative processes entirely, the importance of a careful study of this variation under different environmental conditions is obvious. Shaw shows that the mean size and shape of apples of the Ben Davis variety are distinctly different for different trees of the same orchard and even for the different parts of the same tree. There are very marked differences in apples of this variety in respect to size and shape characters when they are grown under widely different soil and climatic conditions. In the south the Ben Davis is a short round apple; in the north it is an elongated apple. Not only are the means different in different environments, but also the variability (as measured by the coefficient of variation) is changed. This paper of Shaw's, while itself purely descrip-

tive, is of great value not only for the interesting data regarding variation which it presents, but also in indicating clearly the rich reward which may be expected to follow a combined experimental and biometric attack upon the fundamental biological problem of the effect of stock on scion.

In the papers so far discussed there has been in every case some attempt at biometric analysis of the raw statistical data. There are constantly appearing in agricultural literature papers in which a great mass of first-class statistical material on variation and correlation in agricultural plants is presented but not analyzed biometrically, or only incompletely so. Examples of this are found (to mention but two) in the interesting papers of Kohler on potatoes and Westgate on alfalfa. A conspicuous instance of failure to make profitable use of elementary biometrical methods is seen in the paper of Stockberger and Thompson on hops. These authors put their data in form for calculating variation and correlation constants (*e. g.*, they give a correlation table for the correlation between number of vines to the hill and yield per hill) but do not determine the constants.

It is evident from what has preceded that biometrical methods are rapidly gaining a place among the agricultural investigator's working tools. Keeping always in mind the caution expressed at the beginning of this article that biometric zeal be not allowed to outrun biological discretion this movement merits only commendation and further encouragement. The agricultural investigator has an almost unique opportunity to make significant and profitable application of biometric methods of research.

RAYMOND PEARL.

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ON SEX-CHROMOSOMES IN HERMAPHRODITISM

RESEARCHES by Boveri and his pupils have shown in certain nematodes, as in arthropods, the existence of two sorts of spermatozoa, one of which contains one more chromosome or chromosome

component than does the other. Eggs fertilized by the one sort of sperm develop into females, those fertilized by the other sort develop into males, as is shown by a cytological study of the two sexes, the female invariably containing the greater number of chromosomes or chromosome components.

Some results of especial interest have been obtained by Boveri[1] from studies of a little nematode (*Rhabditis nigrovenosa*) which occurs as a parasite in the lung of the frog. A free-living generation alternates with the parasitic one. It has long been known that the parasitic generation consists exclusively of females, but the free-living one of both sexes. According to Leuckart and Boveri, parthenogenesis may occur in the parasitic generation, though it is not the exclusive method of reproduction in this generation. For Anton Schneider, recently confirmed by Boveri, found spermatozoa in the genital tract of the parasitic female, and further established the remarkable fact that these spermatozoa develop in the ovarian tubules of the young female herself, which therefore, though a female in external form, is really a hermaphrodite. The close-fertilized eggs of the parasitic worm develop into embryos which are voided with the feces of the host and form the free-living generation, consisting of sexually separate males and females. These produce in turn, from fertilized eggs, the parasitic generation composed exclusively of hermaphroditic females.

The question which Boveri studied was this—how is sex determined in the parasitic generation? Are the spermatozoa of the self-fertilized mother dimorphic, and if so how do they arise?

First of all he established the fact that the spermatozoa found in the parasitic females are of two sorts. The chromosomes may be counted even in the mature sperm, and were found to be in part of the spermatozoa *six* in number, in part of them *five*. In the egg and polar cells were found always six elements. The fertilized egg therefore must contain either *twelve* or *eleven* chromosomes. From one of the former sort doubtless develops a female, from the latter a male. For in the male of the free-living generation Boveri found 11 chromosomes disposed as follows in the spermatocyte of the first order: 5 tetrads, 1 dyad (x chromosome), an arrangement explained as due to splitting of each of the 11 elements, ten of which were disposed in five pairs, forming

[1] "Ueber das verhalten der Geschlechtschromosomen bei hermaphroditismus," *Verh. d. phys.-med. Gesellschaft zu Würzburg*, N. F., 41, pp. 83–97, 1911.

in their split condition tetrad groups, the eleventh being the unpaired x element, as split a dyad. The x chromosome (dyad) passes entire into one of the spermatocytes of the second order, the end result being the formation of spermatids of two sorts, those which contain six and those which contain five chromosomes.

Now arises the first difficulty. If the male individual forms two sorts of spermatozoa, why are not offspring of *both sexes* produced by the free-living generation, instead of females alone? Boveri finds no evidence of degeneration in the spermatozoa containing only 5 chromosomes, and he finds that both sorts are received by the female at copulation, but assumes that the 5-chromosome sort is for some reason incapable of fertilizing the eggs, because from these develop only females containing 12 chromosomes. He relies here upon an analogy with the case of aphids and phylloxerans worked out by Morgan and von Baehr. In those cases, namely, the spermatids with the smaller number of chromosomes fail to develop. In the present case, though developed, they fail, in Boveri's opinion, to function in the fertilization of the egg.

Now comes the second difficulty. If the cells of the (hermaphroditic) female contain *twelve* chromosomes, how does she form spermatozoa containing *five* chromosomes, which is less than the *half-number?* Boveri finds that it is by a peculiar method of cell-division in spermatogenesis. In oogenesis there appear in the oocyte of the first order 6 tetrads which are distributed equally at the maturation divisions. The egg accordingly always contains 6 elements. But in spermatogenesis, in the same hermaphrodite generation, there form 5 tetrads and in place of the sixth a pair of separate dyads which are identified as x-elements. These lag behind the tetrads in division, so that when the five other elements have been distributed in cell-division these two remain at the equator of the spindle. Boveri was unable to ascertain just what does become of them but he assumes that one spermatid lacks them altogether, and this becomes the *male-determining* sperm. What Boveri failed to observe seems to have been observed by W. Schleip,[2] who finds that one x-element passes into half the spermatids, but the other remains on the spindle and does not enter a spermatid. Hence only half the spermatids contain six elements, the others contain five.

Why one process of reduction occurs in spermatogenesis and

[2] *Ber. d. Naturf. Gesell.*, Freiburg i. Br., 19, 1911.

another in oogenesis is unknown. Boveri makes several suggestions without adopting any of them as (1) position of the cells in the egg-tube, (2) seasonal conditions (sperm-production occurs first, egg-production later), (3) unequal plasmatic cell-divisions in the young worm, differentiating sperm-producing from egg-producing tissue.

As regards hermaphroditic animals in general, Boveri maintains that these, when they have the secondary characters of one sex only have that of the female rather than of the male, citing as examples gastropods and cirripeds. Females may retain the capacity to develop sperm, but males do not retain the capacity to develop eggs. For the male state is due to retrogressive variation, loss of cell-constituents, as for example of an x-chromosome. Now in the female this loss may occur *in certain reproductive cells only*, which then become reproductive cells of the male, *i. e.*, spermatozoa. But in the male individual, since *all* its cells are in the reduced state, reproductive bodies characteristic of the female (eggs) can not be produced. Nevertheless the male, though unable to form eggs (which we may assume can come only from a 2x cell) is able to form female-producing *gametes*, those with the full half number of chromosomes.

In its bearing on general theories of sex-determination Boveri's paper is important. It provides a way of reconciling the opposed views that sex-determination is independent of environmental influences and that it is dependent upon them. Both views are correct in part.

Sex is apparently in all cases controlled by cell structure, a clear index of which is afforded by the number of the chromosomes found in the nucleus. The more complete, or fully duplex, state is in all cases characteristic of the female; a more reduced state, either partially duplex or simplex, is characteristic of the male. But *external conditions* may influence the cell-constitution, and so indirectly determine sex. This is known to be the case in parthenogenesis and according to Boveri's observation in this paper it may be true in hermaphroditism also. Thus in rotifiers and daphnids abundant nutrition causes the unfertilized egg to develop without undergoing reduction, *i. e.*, in the fully duplex (2N) condition, and a female results; poor nutrition causes the unfertilized egg to delay development until maturation is complete and it has passed into the simplex condition, and a male results. The protoplasmic differences in the two cases are not confined to differences in chromosome number, the cell

size is also different, the female egg being larger. But the size-difference is not all-important, either, for the winter egg of the rotifers or daphnids is still larger, yet undergoes complete reduction, but will not develop in this condition unless fertilized; then it produces a female, being in the fully duplex, 2N condition. Sex in such cases is correlated with a particular cell-constitution, but this cell-constitution may be influenced by the environment; hence the environment may *indirectly* control sex.

Boveri's present contribution adds another important case to those previously on record. In the nematode, too, protoplasmic conditions control sex, but it is quite possible that external agencies as yet not identified may in this case also determine those protoplasmic conditions and so indirectly determine sex.

The question naturally arises whether the same may not be true in the higher animals also, those which are sexually separate. This idea has been strongly advocated from time immemorial, and still has its adherents, but a really critical analysis of the evidence shows that it rests on a very insufficient basis. In fact the experimental evidence is almost conclusive against it.

There is no *a priori* reason why the cell structure which differentiates male-producing from female-producing gametes or zygotes should not be controllable through environmental agencies in the higher animals, as in parthenogenetic animals. But *is* it? This is a question of fact, in determining which we must weigh evidence. The really critical examination of such evidence was begun in 1900 by Cuénot in a notable paper published in in the *Bulletin Scientifique*, and has been followed up by several others who have carried out carefully planned experimental researches, as, for example, Oscar Schultze. Their evidence is almost wholly against the idea that sex in the higher animals can be controlled either directly or indirectly. Russo,[3] indeed, still maintains this view. He holds that by feeding or injections of lecithin the structure of the ovule in the rabbit ovary may be altered, and that a female embryo develops from such altered ovules. Now there are two questions of fact involved in this evidence, first whether the cell-structure described by Russo is induced by the lecithin treatment or by some other agency. This is a question for cytologists to answer. The second question is whether the cell structure described has anything to do with sex-determination. This is a question in part for the experimental breeder to answer. From this point of view I have elsewhere

[3] *Biol. Centrbl.*, 1911.

discussed Russo's data. Two independent repetitions of his breeding experiments, one made in Italy, the other in England, have failed to confirm his conclusions, which therefore, as matters stand, have slight weight.

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June 12, 1911.

NOTES ON ICHTHYOLOGY

IN the *Abhandlungen of the Akademie der Wissenschaften*, in Bavaria, Vol. IV, Münich, 1910, Victor Franz has an elaborate account of the bony fishes collected in Japan by Haberer and Döflein. This is an important paper, containing descriptions and figures of numerous new species.

In the Contributions from the Zoological Laboratory of Indiana University, No. 76, part 2, Dr. Carl H. Eigenmann gives a "Catalogue and Bibliography of the Fresh-water Fishes found in Tropical and South Temperate America," including all south of the latitude of the mouth of the Rio Grande. Dr. Eigenmann gives a discussion of the valid reasons which have led him to retain the generic name *Æquidens* in place of *Acara*.

In the *Bulletin of the Bureau of Fisheries*, Vol. XXIX, 1909, Jordan and Evermann discuss the "Salmonoid Fishes of the Great Lakes," with numerous plates, some of them in color. The name *Leucichthys* of Dybowski is adopted in place of the earlier name, *Argyrosomus*, of Agassiz, which was first used for a marine fish. Four new species of *Leucichthys* or lake herring are described, *L. supernas* from Lake Superior, *L. cyanopterus* from Lake Superior, *L. manitoulinus* from Lake Huron, and *L. ontariensis* from Lake Ontario. A new variety, *L. harengus arcturus*, is described from the west end of Lake Superior. Two new sub-generic names are adopted: *Thrissomimus* Gill for the ordinary lake herring, the name *Argyrosomus* being preoccupied; and *Cisco* for the deep-water forms.. In this paper it is shown that the shore lake herring, instead of constituting a single species, are really several in number, at least six of them in the Great Lakes deserving recognition as species.

In the *Bulletin of the Bureau of Fisheries*, Vol. XXIX, 1909, Dr. Charles W. Greene discusses in detail the migration of the salmon in the Columbia River, treating with considerable fullness the methods by which individuals may be marked.

A number of tables are given illustrating the movement of the salmon, an average in the Lower Columbia being about seven and a half miles per day.

In the Bulletin of the Illinois State Laboratory of Natural History, Dr. Stephen A. Forbes gives a table and a series of maps illustrating the distribution of the different species of fishes. as traced in the state of Illinois. One hundred and fifty native species are recognized, all of them represented in the neighboring states, variously extending into the rather monotonous basin of Illinois, in accordance with the character of the water. In the absence of geographical barriers, the causes influencing their distribution are climatic, geologic and ecological. A number of other generalizations are developed.

The British Museum of Natural History has issued the second volume of George A. Boulenger's important "Catalogue of the Fresh-water Fishes of Africa." This covers the catfishes, and a portion of the carp family. Most of the species are illustrated by good drawings.

In the *Annales de L'Institut Oceanographique,* of Prince Albert of Monaco, Dr. Louis Fage gives an account of the many forms of larval fishes taken in the deep-sea work of the Prince of Monaco.

In the *Philippine Journal of Science,* Vol. V, July, 1910, Mr. Alvin Seale describes four new species of fishes from Bantayan Island.

In the *Memoirs of the Indian Museum in Calcutta,* Vol. III, 1910, Dr. N. Annandale and J. T. Jenkins describe and figure numerous fishes taken in deep water by the steamer "Golden Crown."

In the *Memoirs of the Museum of Comparative Zoology,* at Harvard University, Vol. XXVI, 1911, William C. Kendall and Edmund L. Goldsborough record the species of shore-fishes taken by the *Albatross* in the South Seas, when in charge of Professor Alexander Agassiz. Numerous new species are described, and valuable notes are given on those recorded by previous authors.

In the *Proceedings of the United States National Museum,* Vol. 38. 1910, Jordan and Thompson discuss the "Gold-eye of Lake Winnipeg," an excellent food fish which has been generally overlooked by authors, *Amphiodon alosoides.*

In the same *Proceedings,* Vol. 39, 1911, Jordan and Thompson discuss the "Fishes of the Families *Lobotidæ* and *Lutianidæ,*" found in the waters of Japan.

In the same *Proceedings*, Vol. 39, 1911, the same authors discuss the species of the family *Sciænidæ* found in the waters of Japan.

In the same *Proceedings*, Vol. 38, 1910, Barton A. Bean and Alfred C. Weed discuss the "Venomous Toadfishes of South America" belonging to *Thalassophryne* and related genera, with figures of the different species and a discussion of the venomous spines by which they are armed.

In the same *Proceedings*, Vol. 39, 1911, Theodore Gill discusses the "Structure and Habits of the Wolffishes." The genus *Lycichthys*, based on *Anarrhicas latifrons*, is here fully defined. A new species, *Lycichthys fortidens*, from the North Atlantic, is described and figured.

In the same *Proceedings*, Vol. 38, 1910, William Converse Kendall describes a collection of fishes made in Labrador by Owen Bryant. Among these are certain sea trout not belonging to the ordinary brook-trout species, *Salvelinus fortinalis*. The species in question is provisionally identified as *Salvelinus stagnalis*, but it is possible that it is a species still undescribed. The name *Salmo immaculatus* was probably originally given to this species, but the name is preoccupied.

In the same *Proceedings*, Vol. 38, 1910, Barton W. Evermann and William C. Kendall compare the chub-mackerels, *Scomber colias*, of the Atlantic, with those of the Pacific, called *S. japonicus*. They find the two species different, in measuring the specimens examined, the head being especially larger in the Pacific fish—about $3\frac{1}{4}$ instead of $3\frac{2}{3}$ in the length of the body. Comparison of other specimens made at Stanford University does not seem to bear out these differences, and the propriety of separating the Atlantic species from the earlier named Japanese form as *Scomber colias* is still doubtful.

In the same *Proceedings*, Vol. 37, 1910, Barton A. Bean and Alfred C. Weed discuss the Japanese genus *Anteliochimæra*, in which they show that the genus is probably identical with *Harriotta*, an Atlantic genus of *Chimæra*.

In the same *Proceedings*, Vol. 39, 1910, Barton W. Evermann and Homer B. Latimer give a "Catalogue of the Fishes," forty in number, known to inhabit the Lake of the Woods.

In the *Annals and Magazine of Natural History*, November, 1910, C. Tate Regan discusses the families of Zeidæ and Caproidæ.

In the same *Annals* Mr. Regan discusses the origin and evolution of the order of the flounders. He regards them as descended

from perchlike fishes—the genus *Psettodes* with a spinous dorsal, being the most primitive of the group. He divides the flatfishes into four families, Bothidæ, Pleuronectidæ, Soleidæ and Cynoglossidæ. He finds no evidence that the flounders are related to *Zeus*, as suggested by Boulenger. The relation to the fossil genus *Amphistium* seems to be possible. In Regan's judgment this fish is a percoid, allied to *Psettus* or to *Platax*. The adjustment of the genera of flounders is somewhat different from that usually accepted.

In the *Proceedings of the Biological Society of Washington*, Professor T. D. A. Cockerell discusses the scales of various soft-rayed fishes. He finds in the structure of the scale valuable characters for the distinction of genera and subgenera, in different groups of fishes. This is the first critical study of scales with a view to using their characters in the classification of genera, and Mr. Cockerell's observation should be extended throughout ichthyology.

In the *Bulletin of the American Museum of Natural History*, Vol. XXVIII, 1910, John Treadwell Nichols discusses the occurrence of the pelagic pipefish, *Siphostoma pelagicum*. They occur especially in the drifting Gulf weed of the mid-ocean. Mr. Nichols has also examined the type of *Caranx forsteri* from the Ile de France. He considers that this species is identical with the *marginatus* of Gill; the *rhabdotus* of Jenkins; and the *elacate* of Jordan and Evermann. The specimen called *forsteri* in Jordan and Evermann's Hawaiian report, he thinks identical with the Atlantic species *latus*.

In the *Bulletin of the American Museum of Natural History*, Vol. 28, John T. Nichols describes two new blennies from Florida, *Stathmonotus tekla* from Key West, and *Blennius fabbri* from Miami.

In the *Annals and Magazine of Natural History*, 1910, Holt and Byrne describe a new deep-water fish as *Grammatostomias flagellibarba*.

In the *Bulletin of the American Museum of Natural History*, Vol. XXVIII, 1910, Russell J. Coles describes an interesting collection of fishes from Beaufort, N. C. One of these is *Mobula olfersi*, the small devil fish. Several other rare West Indian species are recorded by Mr. Coles.

In the AMERICAN NATURALIST, 1909, E. W. Gudger records a number of species of interesting fishes found also at Beaufort.

In the *Proceedings of the Royal Society of Queensland*, 1910,

Mr. J. Douglas Ogilby describes a number of new species of fishes from the neighborhood of Brisbane.

In the *Notes from the Leyden Museum,* Vol. XXXII, Professor Max Weber describes a number of new species of fishes from New Guinea.

In the *Revista do Museu Paulista,* Vol. VIII, 1910, Professor Rodolpho von Ihering describes a number of new catfishes from the neighborhood of São Paulo, in Brazil.

In the *Bulletin of the American Museum of Natural History,* Vol. XXX, 1911, Dr. Charles H. Gilbert describes a number of lantern fishes. One of them, *Lampanyctus nicholsi,* is new, taken near the Falkland Islands.

In *Science,* Vol. XXXI, Dr. George Wagner, of the University of Wisconsin, describes a new Cisco, from Lake Michigan, under the name of *Argyrosomus johannæ.* Of this species a colored figure is given by Jordan and Evermann in the article noticed above.

In the *Annals of Scottish Natural History,* January, 1911, Mr. C. Tate Regan discusses the giant pike of Loch Ken, in Scotland, which reaches a weight of over seventy pounds.

In the *Annals and Magazine of Natural History,* Vol. VII, Mr. Regan discusses the "Systematic Position of the Genus *Macristium.*" *M. chavesi* is a deep-water fish which represents a family related to *Alepocephalus.*

In the same *Annals,* Vol. VIII, Mr. Regan discusses the "Lampreys of the World." He regards *Bathymyzon* as an ordinary lamprey with the teeth feeble. In *Ichthyomyzon* he recognizes two species, *bdellium* and *castaneus,* rejecting the name *concolor* as being based on a larva, perhaps of *Lampetra.* The species, *spadiceus, japonicus* and *wilderi* are referred to the genus *Entosphenus* instead of *Lampetra.*

In the *Annals of the Carnegie Museum,* Vol. VII, 1910, Dr. Jordan describes a series of fossil fishes belonging to the Carnegie Museum, and obtained by Dr. John C. Branner in Brazil. These fishes are from Eocene rocks at Riacho Doce in Brazil. Two new genera are described, *Ellipes* and *Dastilbe,* both of these being based on diminutive herring.

In the *Transactions of the New Zealand Institute,* Vol. XLII, 1909, Edgar R. Waite gives a "Catalogue of Fishes from Kermadec and Norfolk Islands."

In another paper in the same *Annals* he gives notes on various New Zealand fishes.

In the *Annals of the Carnegie Museum,* Vol. VII, Jordan and

Thompson describe a collection of fishes made by Professor J. F. Abbott at Irkutsk in Siberia. Several figures of rare species are given.

In the *Proceedings of the Biological Society of Washington*, William C. Kendall shows that the trout-perch should be called *Percopsis omiscomaycus*. The forgotten name of Walbaum (*Salmo omiscomaycus*) clearly belongs to this curious fish.

In the "Fortieth Annual Report of the Fisheries of Rhode Island," Dr. Henry C. Tracy gives a list of the fishes known to inhabit that state. Among these are several rare forms from the West Indies.

In *Science*, Vol. XXXII, George Wagner discusses the stickleback of Lake Superior, and shows that *Eucalia pygmæa* from Lake Superior is not distinct from the ordinary *Eucalia inconstans*.

In the *Bulletin of the American Museum of Natural History*, Vol. XXIII, 1907, Newton Miller describes the fishes of the Montagua River in Guatemala. The following new species are recorded: *Pœcilia amates, Thyrina meeki, Cichlasoma spilurum, Cichlasoma globosum, Cichlasoma mañana, Cichlasoma acutum*.

In the *Arkiv for Zoologie* Band 4, Ribeiro describes some catfishes from the Iporanga River, near São Paulo in Brazil.

In the *Proceedings of the Biological Society of Washington*, Barton W. Evermann and T. D. A. Cockerell describe three new species of minnows, *Richardsonius thermophilus* from Warm Springs, Ore.; *Notropis kendalli* from Cross Lake Thoroughfare, Me.; and *Notropis universitatis* from Boulder, Col.

In the same *Proceedings*, Mr. Cockerell and Mr. Otis Callaway describe the scales of various minnows of the United States. A subgenus, *Coccogenia*, is established for *Notropis coccogenis*.

In the *Annals and Magazine of Natural History*, Vol. VII, 1911, Mr. Regan discusses the families of Berycidæ and their relationship. He proposes to regard the Berycomorphi as forming a distinct order, and a second order, *Xenoberyces*, is established for the Stephanoberycidæ, Melamphaidæ and other relatives.

In the *Proceedings of the United States National Museum*, Vol. 38, 1910, Professor E. C. Starks and W. F. Thompson review the flounders of the genus *Pleuronichthys*, with two new species, *P. nephelus* from San Juan Islands, Puget Sound, and *P. ocellatus* from the Gulf of California.

In the *Annals and Magazine of Natural History*, Vol. VII, 1911, Mr. Regan discusses the "Anatomy and Classification of the Teleostean Fishes of the Order Iniomi," bringing the various

groups into clearer relations with each other. He places the genus *Ateleopus* among the Iniomi.

In the *Philippine Journal of Science*, Vol. V, 1910, Alvin Seale describes a collection of fishes from Borneo.

In the *Proceedings of the Academy of Natural Sciences of Philadelphia*, April, 1910, Henry W. Fowler describes and figures the types of many species of American fishes of the genus *Notropis*.

In the same *Proceedings*, Mr. Fowler describes *Paralepis barracudina*, a new species from Corson's Inlet, New Jersey.

In the same *Proceedings*, Mr. Fowler describes various little-known fishes from New Jersey, and also a number of new species of ganoid fishes. He divides the garpikes into two genera, *Lepisosteus* and *Cylindrosteus*. Instead of the three species usually recognized, Mr. Fowler discussed twelve. It has been evident for some time that the number of species in this group is much greater than the three admitted by Jordan and Evermann. The value of the different species defined by Mr. Fowler, however, is yet to be proved. It will be necessary to have a very large amount of material before these questions of identity can be fully decided.

The species recognized by Mr. Fowler are: *Lepisosteus huronensis, L. osseus, L. treculii, L. clintonii, Cylindrosteus platostomus, C. scabriceps, C. productus, C. agassizii, C. castelnaudii, C. megalops, C. tristœchus, C. tropicus.*

In the same *Proceedings*, Mr. Fowler describes *Dixonina nemoptera*, a new species of albuloid from Santa Domingo. This genus differs from Albula in having the last ray of the dorsal and anal filamentous.

In the *Proceedings of the National Museum*, Vol. 40, 1911, W. C. Kendall describes two very rare species of sole, *Gymnachirus fasciatus*, from Long Key, Fla., and *G. nudus* from Tisbury Great Pond, on Marthas Vineyard. Both are doubtless strays from the Gulf Stream.

In the *Bulletin of the University of California*, Geology, Vol. V, James Z. Gilbert describes a fossil flounder, *Evesthes jordani*, notable for its large mouth, from Miocene rocks near Lompoc, in California. This is one of the oldest-known of fossil flounders, and its relations are evidently with the halibut tribe, and with the genera still represented on the California coast.

In *Science*, Vol. 30, H. H. Newman shows clearly that the killifish *Fundulus majalis* is never viviparous.

In the *Proceedings of the United States National Museum* for

1911, Barton A. Bean and Alfred C. Weed discuss the habits of the electric ray, *Narcine brasiliensis.*

In the same *Proceedings,* for 1911, Dr. Hugh M. Smith and Lewis Radcliffe describe three new species of butterfly fishes from the Philippines.

In the *Mémoires de l'Académie Royale des Sciences et des Lettres de Danemark,* Dr. Hector F. E. Jungersen describes in great detail the anatomy of the pipefishes and trumpet fishes, and their relatives. In this, numerous errors of interpretation made by different authors are corrected, and the paper is one of high merit.

In the *Annals and Magazine of Natural History,* Vol. VII, 1911, Mr. C. Tate Regan discusses the fishes related to the silver gar and flying fish, in the order of Synentognathi. He recognizes two suborders, the one containing the families of Belonidæ and Scomberesodinæ, the other containing the Hemirhamphinæ and Exocœtidæ. He suggests the close relation or possible identity of the fossil genus *Cobitopsis* with *Chriodorus.* Regan regards *Esox lucius,* the supposed *Esox* of Pliny, as the type of *Esox.* He retains *Belone* for the European silver gar, rejecting *Ramphistoma* as a nomen nudum.

In the same *Annals,* Mr. Regan describes the new order Microcyprini, containing the Amblyopsidæ and the Pœciliidæ, each of which families represents with him a distinct suborder. This leaves in the order of Haplomi only three families, the Esocidæ, Umbridæ and Dalliidæ. He thinks that the Haplomi are related to the isospondylous fishes, while the Microcyprini are nearer to the Synentognathi. Mr. Regan notes that the genera *Retropinna, Microstoma* and *Salanx* lack the mesocoracoid characteristics of the other salmon-like fishes. Nevertheless, he regards these along with the fresh-water trout-like fishes of the southern hemisphere, the Galaxiidæ and the Haplochitonidæ, as true Salmonoids, although these latter have also lost the mesocoracoid. The fossil family of Enchodontidæ, Regan regards as an ally of the Stomiatidæ. The Kneriidæ he regards as near to the *Chanidæ.* Regan regards *Panchax* as a genus distinct from *Aplocheilus. Aplocheilus* originally contained two distinct types, but the name was definitely restricted by Bleeker to the group having no vomerine teeth. *Oryzias,* which belongs to the latter group, Regan regards as a synonym of *Haplochilus.* Apparently the short jaws of *Oryzias* should distinguish it from *Aplocheilus,* though it may be identical with some of the African genera.

In the same *Annals,* Mr. Regan discusses the order of Salmo-

percæ. Beside *Percopsis* and *Columbia,* he adds to this group a genus *Aphredoderus,* this form without an adipose fin constituting a distinct family. He notes that the study of the anatomy of the last genus does not indicate any real affinity with the sunfishes.

In the same *Annals,* Mr. Regan discusses the allies of the genus Cirrhites. In this group he finds five distinct families.

Over thirty years ago, when the great house of Godeffroy, of Hamburg, was dominating the trade of the South Seas, this company undertook the establishment of a natural history museum in Hamburg, and with this the publication of a journal called the *Journal des Museum Godeffroy,* in which the life of the South Seas should be set forth. This journal was sumptuously printed, and illustrated with expensive colored plates. One of the important articles was that descriptive of Andrew Garrett's Fische der Südsee, Andrew Garrett having made an extensive collection of fishes in various islands, and having made colored paintings of a large number of the species. During the time, 1876–1881, the first two volumes of the Fische der Südsee appeared, the author being Dr. Albert Gunther, keeper of the British Museum. The work ended abruptly in the middle of the family of *Labridæ.* The great house of Godeffroy, having undertaken in Europe enterprises beyond its control, went into collapse, and the publication of its journal was suspended. In 1909, under the management of Friedrichsen & Company (publishers), the work has been resumed and brought to completion, with the assistance of Mr. C. Tate Regan, of the British Museum. This has been made possible by the "munificence of the family of Dr. Wilhelm Martin von Godeffroy."

This completed work is a monument to the industry and keen intelligence of Dr. Gunther, and it is the most important treatise concerning the fishes of the region between Hawaii and Borneo known as the South Seas. In the different papers by Jordan and Evermann, and their associates, Snyder, Fowler and Seale, much of the same ground has been covered, and Dr. Günther gives special credit to "the energy" of these American authors in their investigations, particularly of the Hawaiian and Samoan archipelagos. Comparing this work with Jordan & Seale's "Fishes of Samoa," we find a general agreement on all matters where adequate material is present. The American writers generally have given proposed new species the benefit of doubt, by not reducing them to synonymy until it is shown that the new name is a mere synonym. On the other hand, Dr. Günther has

consistently left new species in synonymy unless their right to independent rank has been made clear. In general, the British Museum publications have been characterized by the assumption that a species is not valid until it is represented in the collections of the museum. There is room for many differences of opinion in regard to the relation of certain forms, and in regard to matters of nomenclature, but there can be no difference of opinion as to the great value of this work, and as to the accuracy of these fine plates, most of these being copies of the colored drawings of Mr. Garrett.

In the *Zoological Magazine* of Tokyo, Dr. Kishinouye has a paper on the Sparoid fishes of Japan. It is probably a valuable paper, but, being written almost entirely in Japanese, it becomes inaccessible to naturalists of the rest of the world, and it is hoped that this will not establish a precedent, at least unless a résumé in some modern language can accompany the descriptions of new species, and the new material which the writer is able to add.

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SOME RECENT BOOKS ON FOSSIL PLANTS

THE appearance within two years of three general works on paleobotany, is a sufficiently marked indication of the great interest which this phase of botany at the present time is exciting in England.[1] Much of the most important work which is now being published by the British botanists deals with fossil plants.

The English botanist is in some respects at a great disadvantage compared with his American colleagues. The comparatively meagre flora of the British Islands has already been exhaustively studied, and is a strong contrast to the extensive and varied flora of North America, which, except in the older parts of the country, still offers a rich field to the systematist and plant-geographer, as well as to students of morphology and physiology. This difference in the natural advantages of the two countries no doubt explains to some extent the greater interest in fossil plants shown by the English botanists. But unquestionably much more important is the availability of great collections of important fossils awaiting investigation; and the important

[1] Scott, D. H., "Studies in Fossil Botany," 2 vols., London, Adam and Charles Black, 1908–9. Seward, A. C., "Fossil Plants," Vol. II, Cambridge University Press, 1910. Stopes, Marie C., "Ancient Plants," Blackie & Son, London, 1910.

results already obtained by workers in this field offer great inducements to the young botanist. It must not be inferred that no interest is shown in the study of fossil plants by American workers, but paleobotany has not received the same attention here as in England.[2]

The many important contributions to the study of fossil plants by Scott and Seward are familiar to all students of paleobotany, and their treatises have the stamp of authority. Miss Stopes has published papers of much value, and her little volume presents in clear and fairly untechnical language some of the most important topics of the science. While the books of Professors Scott and Seward are designed primarily for botanical students, and are necessarily technical in their treatment, Miss Stopes's volume is intended mainly for the layman, and seems well suited to its purpose.

Professor Scott's two volumes deal almost entirely with the vascular plants, especially the Pteridophytes, which, as might be expected from the author's intimate knowledge of these forms, are handled in a thoroughly adequate fashion. The first volume treats of the Pteridophytes proper, while the second deals with the seed-bearing forms, including a very full and satisfactory treatment of those seed-bearing ferns, the "Pteridosperms" or "Cycadofilices," the investigations of which during the last ten or fifteen years have made such profound changes in our conceptions of the nature of the fern-like plants of the Paleozoic.

The Cycads and their fossil relations, the Benettiteæ, or Cycadeoideæ, are also treated at length, and the Cordaitales receive ample treatment; but the Conifers are passed over very briefly, and no account at all is given of the fossil Angiosperms, a group which is in woeful need of careful treatment by competent investigators.

Professor Seward's work is on a somewhat larger scale, and takes into account the whole vegetable kingdom. The work is, however, incomplete as yet. The present volume, the second of a proposed series of three, is devoted mainly to the Lycopods and ferns. The former volume comprised the Thallophytes and Bryophytes, together with the most of the Equisetineæ. The third and concluding volumes proposes to deal with the seed-bearing plants, including the Pteridosperms.

[2] In Coulter and Chamberlain's recent valuable treatise on the Gymnosperms, the fossil forms are treated at length, and this section of the book is one of its most valuable features. The important work of Wieland, Jeffry and other students of fossil plants in America must not be overlooked.

With these three books, at the same time reliable in their statements, and attractively written, English and American students can have no excuse for ignorance of the present status of paleobotany.

The attitude of botanists toward the study of fossil plants has undergone a marked change of late years. It is now no longer true that the students of fossil plants know little or nothing about living ones, and the great advancements of late years are largely due to the fact that recent students of fossil plants are thoroughly trained botanists. Moreover, as in other branches of botany, greatly improved methods have been developed, and the microscopic study of sections of petrified plant-tissues now make it possible in many cases to examine accurately the tissues of the fossil plants, and to compare them with the living forms supposed to be related to them. The perfection of some of these sections of fossil tissues is quite astonishing.

Of course it is the firmer tissues, like the epidermis and woody structures of the vascular plants which are most commonly preserved, and it is not strange that the paleobotanist should lay great stress upon the importance of the vascular skeleton which is so perfectly preserved. Students of living plants sometimes think that the great morphological importance attributed to the vascular system has been rather exaggerated, and there is no question that some of the far-reaching conclusions drawn from what to the layman seems very inadequate evidence, are not justified when they are taken in connection with the evidence furnished by a study of living forms. One can not accept without reserve many of the conclusions drawn from the study of fragmentary material, often very badly preserved. Nevertheless, no one can dispute that great advances have been made in our knowledge of the history of the development of the plant kingdom resulting from the discoveries made by students of fossil plants.

The problems which confront the student of fossil plants, and the difficulties which he encounters, are well set forth in the introductory chapter of Dr. Scott's book. The extremely fragmentary character of the record, and especially the great difference shown by different periods in the preservation of plant remains, are clearly set forth. The Carboniferous, as the students of fossil plants are aware, affords the richest fossil flora known, and it is especially with the Carboniferous flora that Dr. Scott concerns himself.

As it is among the Paleozoic Pteridophytes that we are to

look for the ancestors of the modern seed-bearing plants, the rich pteridophytic flora of the Carboniferous naturally takes first place, and it can be readily understood that an absorption in the study of these interesting fossils should perhaps overshadow the importance of other forms. One can not help feeling that if the search for remains of the Bryophytes in the Paleozoic rocks had been pursued with the same zeal as has been shown in the study of the vascular plants, something more than the extremely fragmentary evidences of their existence would be forthcoming.

Professor Seward, in his first volume published in 1898, has given an admirable account of the different methods of fossilization, and also the distribution of fossils. He points out in a very interesting and convincing way the evidences of the existence of the same factors at work at the present day as in times past. Perhaps the most striking fact brought out in the distribution of plant remains is the at first puzzling occurrence of freshwater and land plants in deposits of evident marine origin. Professor Seward, however, shows that the great rivers of to-day, like the Amazon and the Mississippi, are carrying out to sea rafts of vegetation which may very well at some distant time be discovered as fossils covered by marine deposits, to puzzle the geologists of that future epoch.

The history of the fossil Thallophytes remains very much as it was at the time Professor Seward's first volume was published, a rather significant comment on the neglect of these important plants when compared with the great advances made in our knowledge of the fossil Pteridophytes and Gymnosperms during the past decade.

As most of the Thallophytes, especially the algæ, are extremely delicate and perishable organisms, the rarity of recognizable fossil remains is not to be wondered at. Where there is a calcareous incrustation, as in the coralline algæ and many Siphoneæ, very perfect fossils have been preserved. The latter group is especially well represented in a fossil state and has received considerable attention from the paleobotanists. Some of these Siphoneæ can be traced back to the Silurian, and the order is evidently a very old one. A study of these algæ shows that, as at the present day, they played a by no means unimportant rôle as reef-builders.

Among the most characteristic of fossil plants are the Diatoms. While these have left enormous deposits of their flinty shells in the Cretaceous and later rocks, they are practically unknown in

the earlier formations. It is highly probable that in spite of their simple structure the Diatoms are really comparatively recent types. Their enormous numbers and practically universal distribution at the present time, indicate that they are admirably adapted to existing conditions. They particularly abound in the Arctic and Antarctic seas.

While the Fungi are rarely preserved in a very satisfactory condition, there is abundant evidence of their presence in the Paleozoic rocks.

The geological history of the Bryophytes is in a very unsatisfactory condition. Of the liverworts only a few impressions are recorded, and these, according to Seward, are all from Mesozoic or Tertiary formations, and so closely resemble the living species that they throw no light upon the early history of the group. Very few fossil remains which can with certainty be referred to the true mosses are known, but the possibility of confusing the remains of mosses with small Lycopods or even fragments of coniferous branches has to be taken into account.

It has been suggested that the very small number of unmistakable Bryophytes which has been recorded in a fossil state might be explained in the same way as we have suggested for the absence from the Paleozoic rocks of Diatoms; but the cases are hardly parallel since the Bryophytes, particularly the liverworts, give every evidence of being old and generalized types, and do not appear to be particularly well adapted to modern conditions, except as these duplicate what we may assume to have been the conditions during the Carboniferous. It is only in the extremely moist, even climate of the mountain tropics, where the other Paleozoic type, the Pteridophytes reaches its greatest luxuriance, that the liverworts form a conspicuous feature of the flora. Moreover, the liverworts are far less plastic, the number of species, even of wide-spread genera (except in the leafy forms) being usually very small. Both their distribution and their structures point unmistakably to their being a primitive group.

The absence of liverworts from the early geological formations can most readily be explained on the score of their great delicacy, which would prevent their being preserved in a recognizable form. Even were we to admit that the liverworts are modern types, we should still have to explain why their progenitors, and the presumably similar progenitors of the ferns, have not been found in a fossil condition. A parallel case is found in the Cretaceous and Tertiary formations, where the great deposits

of perfectly preserved plant remains are almost entirely referable to trees and shrubs, while the host of herbaceous plants, like the grasses and delicate herbs forming the carpet of the forests, are conspicuous by their absence. If magnolias and maples were abundantly developed in the Tertiary forest, we may be sure that there were also buttercups and violets, although we have no impressions of their leaves and flowers. The same explanation for the extreme scarcity of impressions of herbaceous plants in the Cretaceous and Tertiary formations may be applied to the much more delicate hepatic flora of the Paleozoic.

In the light of comparative morphology, we think most botanists will agree that it is in the highest degree probable that the simpler liverworts, like *Aneura* and *Pellia,* are extremely ancient types, which, like the majority of the algæ, owing to their very delicate and perishable tissues, simply have failed to leave recognizable fossil traces. The only structures of the liverworts which one might hope to recognize in a fossil state are the elaters. It may be that a careful examination of sections of the masses of petrified vegetation resulting from the débris of the Carboniferous forests, may show liverwort elaters, but as yet no such discovery has been recorded. It is also by no means impossible that among the numerous beautifully preserved leaf impressions of the Paleozoic ferns, some might under specially favorable conditions show traces of epiphyllous liverworts, such as are common on fern leaves at the present day in wet tropical forests.

It is the Pteridophytes and their allies among the simpler seed-bearing plants that have largely monopolized the attention of the paleobotanists during the past decade or two. The results of these investigations have been to quite readjust the views long held as to the real nature of many of the Paleozoic fossils. These changes have been mainly among the fern-types, although among the Equisetineæ and Lycopods there have also been important discoveries.

The history of the fossil Equisetineæ need not be dwelt upon here. It is sufficiently well known that this class, at the present day reduced to some twenty-five species belonging to the single genus *Equisetum,* was an important factor in the rich Paleozoic flora. Professor Scott, in the first volume of his studies, gives an excellent account of the present status of our knowledge of this class.

The Lycopods, also a comparatively degenerate group at the present day, showed much greater range of structure and size than at present. The most important discovery of late years

among the fossil Lycopods is the fact that some of the great fossil club-mosses, *e. g., Lepidocarpon,* bore unmistakable seeds. This adds one more instance of the independent origin of seeds in quite unrelated orders of Pteridophytes.

It is among the ferns, however, that the interest of the paleobotanist has been especially centered, both in England and on the continent. The abundance and perfection of the fern-like fossils of the Paleozoic, especially those of the Carboniferous, are sufficiently familiar, but a very large percentage of them are merely impressions of sterile fronds. Numerous investigations of these supposed fern-leaves have proved beyond question that they are not ferns in the strict sense of the word, but are the sterile leaves of fern-like plants which bore true seeds. It has become apparent that these seed-bearing ferns, "Pteridosperms," formed a very important feature of the Carboniferous flora, perhaps outnumbering the true ferns. Indeed, some enthusiastic students of these interesting plants have gone so far as to doubt whether true ferns existed at all at this period!—a conclusion with which it is needless to say few botanists would be inclined to agree. True ferns must have preceded Pteridosperms, and it is hardly likely that none of them should have left fossil remains, not to mention the fact that many of the fossil fronds bear sporangia of whose true fern nature there can be no reasonable doubt.

Of the living ferns, the Marattiaceæ are best represented among the Paleozoic fossils, and their primitive nature is also shown by a study of their structure and development. Most of the Pteridosperms were probably derived from ferns of this type, and it is in many cases apparently not possible to decide whether certain leaves bearing sporangia of the Marattiaceous type are true ferns, or whether they represent the microsporangia of some Pteridosperms. It does not follow, however, as some students of Pteridosperms have argued, that because the sporangia of one doubtful Marattiaceous fern have been shown to belong to a Pteridosperm, that therefore we must suspect all of the sporangia of the Marattiaceous type.

The geological history of the other living family of the eusporangiate ferns, the Ophioglossaceæ, is extremely unsatisfactory. The great rarity of recognizable fossils belonging to this family may perhaps be explained by the perishable nature of their leaves. The soft leaves of *Ophioglossum* and *Botrychium* and the absence of indurated cells from the sporangium would make these plants very poorly fitted for preservation in a fossil state.

It is, however, by no means impossible that some of the earliest known ferns, the Botryopterideæ, may have been related to the Ophioglossaceæ. Both the form of the leaves, and the sporangia which were borne on special leaf segments, are suggestive of the Ophioglossaceæ, and there are also certain anatomical resemblances.

One of the earliest fern-like fossils is the Devonian genus *Archæopteris*. This fossil in the venation of the leaves suggests the simpler types of *Botrychium*, and the sporangia are borne on special leaf segments, which, however, it must be said more nearly resemble *Osmunda* than they do *Botrychium*. Professor Seward is inclined to believe that the sporangia of *Archæopteris* are really pollen-sacs of a Pteridosperm, stating that they are much larger than the sporangia of any known fern, being two or three mm. in length. It is evident that Professor Seward overlooked the Ophioglossaceæ in making this comparison, and it is with these that the comparison really should be made. The sporangia of *Archæopteris* are described as pear-shaped sacs, two to three mm. in length. These are nearly equalled in size by some species of *Botrychium*, such as *B. Lunaria* and *B. silaifolium*, in which the globular sporangia may be 1.5 mm. in diameter, while the sporangia of the large species of *Ophioglossum* very much exceed in size these figures. In *O. pendulum* the sporangia are probably larger than those of any other living Pteridophyte, and may reach a diameter of four millimeters. It is clear then that the mere question of size is not a valid argument for considering *Archæopteris* a Pteridosperm rather than a homosporous fern.

The evidence of the fossil record entirely bears out the conclusions based upon a study of the living ferns that the condition in which the sporophyll, or parts of it, are entirely devoted to spore-production, as in *Ophioglossum* and *Osmunda*, is a more primitive condition than that in which the sporangia are produced upon the backs of unmodified leaves.

There is abundant evidence from a study of existing Archegoniates that the sporophyte of the fern is the result of the elaboration of the sporogonium of some bryophytic ancestor. This being the case, it necessarily follows that the sporophylls are older phylogenetically than the sterile leaves, and are not secondary modifications of the latter. It is to be hoped that students of the Botryopterideæ and other archaic fern types will make a thorough comparison of these with the existing Ophioglossaceæ, in the light of the most recent developmental studies

on the latter. Whether or not we admit the relationship of *Ophioglossum* with these ancient ferns, there is no question that both in regard to the early history of the sporophyte and in the structures of the adult sporophyte, *Ophioglossum* most nearly represents among living ferns what we may fairly assume to have been the primitive type from which the higher ferns have sprung.

In view of the abundant evidence of the primitive nature shown by the living Ophioglossaceæ, we can not believe that these plants did not exist in the earlier geological epochs; and the failure to record them is due either to the complete disorganization of their delicate tissues, or to a failure by investigators to recognize the ferns allied to them which may have been found in a fossil state.

Dr. Scott in his second volume gives an excellent account of the Cordaitales and the Cycads, but it is to be regretted that his treatment of the Conifers is so brief. He explains this by stating that the present knowledge of the fossil Conifers is not sufficiently exact to make a satisfactory general treatment feasible. It is to be hoped that in the concluding part of Professor Seward's treatise they will receive adequate attention.

The Cordaitales, the earliest known seed plants and completely extinct at the present time, are remarkable for the perfection with which their floral structures, as well as their vegetative tissues, have been preserved. They evidently represent a more or less synthetic type with apparent connections with several of the other great groups, but their exact place in the system is still not quite satisfactorily settled.

The advance in our knowledge of the "Cycadophytes"—the Cycads and their relations—during the past ten years has been very great, largely due to the labors of an American paleobotanist, Dr. Wieland.[3] His remarkable studies on the wonderfully preserved Mesozoic Cycads of the Black Hills Region of South Dakota and Wyoming, form one of the most notable contributions to fossil botany that have been made for many years. These Mesozoic Cycads are separated from the recent type of Cycads as a distinct family, the Benettiteæ or Cycadeoideæ. It is the floral structures of these plants that have attracted the greatest attention, as they show a curious similarity in their general structure to such a flower as a magnolia, although they are gymnosperms. This resemblance is so striking that some stu-

[3] Wieland, G. R., "American Fossil Cycads," Carnegie Institution of Washington, Publication No. 34, 1906.

dents have even gone so far as to assume an origin for the lower Angiosperms from some similar type. Much more evidence, however, is necessary before so startling a theory can be accepted.

Professor Scott gives only a brief summary of the fossil history of the Conifers. The order can be traced back to the Permian and it is possible that some types are still older. The oldest recognizable Conifers were apparently allied to the modern Araucarias, and it may be noted in this connection that Seward has expressed the opinion that the Araucariaceæ show sufficient similarity to the Lycopods to warrant the hypothesis that they may have descended from some of the great seed-bearing Lycopods of the Carboniferous. True Araucariaceæ occur from the Triassic, and probably existed in still older formations.

The Taxodineæ to which our bald cypress and Sequoia belong, may go back to the Permian, but there seems to be some doubt of the real relationships of the earliest fossils placed in this family. The Abietineæ, *i. e.*, the pines and firs, do not occur before the later Jurassic and early Cretaceous formations, and the true cypresses seem to be of about similar age. The Taxaceæ, the Yew family, is apparently the most recent of the Conifers, not being found below the Cretaceous.

The geological history of the Angiosperms is very incomplete, and they have received very much less attention than the Pteridophytes and Gymnosperms which have so largely monopolized the attention of the paleobotanist. It would seem as if a critical investigation of the abundant Cretaceous and Tertiary remains of the Angiosperms, comparable to the many complete studies on the Paleozoic and Mesozoic Pteridophytes and Gymnosperms, should yield results which would throw some light upon the origin of the predominant plant-type of the present day.

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UNIVERSITY OF VIRGINIA

INTRODUCTORY, WITH A STATEMENT OF PROBLEMS INVOLVED

THE comparative histologic study of pigmented skins was undertaken with the hope of discovering evidence that might throw more light on the problem of color inheritance among the descendants of crosses between whites and negroes. The primary point at issue, until very recently, was whether human skin color in inheritance conformed more closely to the alternative (Mendelian), or the blended scheme; or perhaps to the ancestral (Galtonian) scheme. The studies of G. C. and C. B. Davenport show conclusively that there is a measure of segregation among the individuals of the third generation, hence a Mendelian-like inheritance.

This study, suggested to me by the above-mentioned investigators, is, consequently, more especially an attempt to test, as critically as microscopic data will allow, the theory of discrete unit characters in color inheritance (discontinuity theory; segregation theory), as opposed to the theory of continuity of the pigment character with interruption of the pigmentation process at

various stages. The study involves two incidental problems: (1) Source of the epidermal pigment, (2) cause of degree of coloration of skin. These matters must receive consideration first. Then follows a discussion of the bearings of the determined facts on the question of color inheritance in crosses between whites and blacks, or mulattos.

Material.—The material studied comprises 18 pieces of skin taken from near the mid-line of the abdomen, including 5 pieces from full-blooded negros of varying grades of color, 6 pieces from mulattos of various shades, 4 pieces from brunets, 2 from blonds, and 1 piece

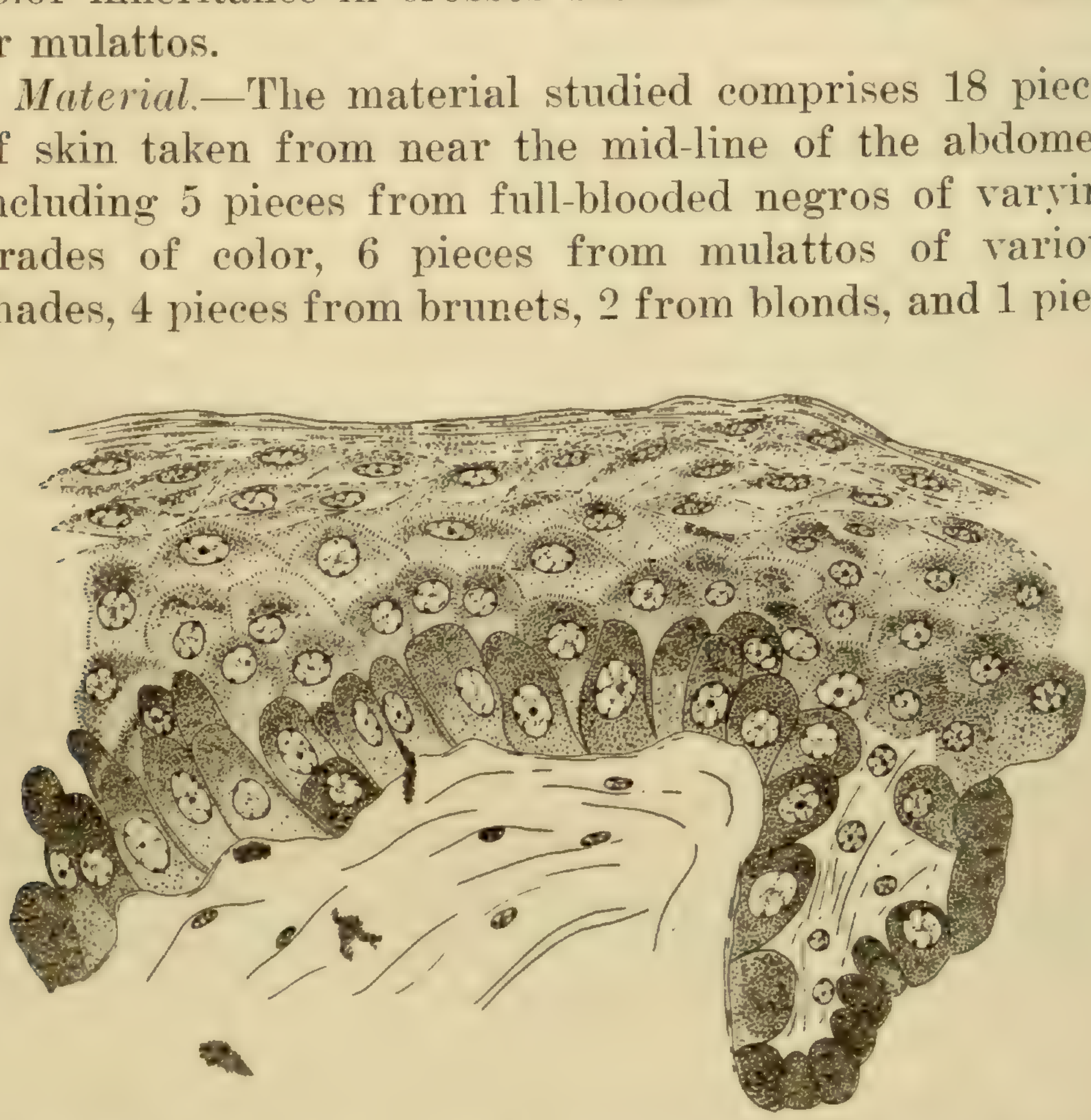

FIG. 1. Camera lucida drawing of unstained section of negro skin (specimen No. 14), showing the distribution of the pigment granules in the epidermis. Nuclei drawn according to their appearance in stained preparation. Dermal pigment cells very much more abundant than would appear from this particular region. The greater height of the basal cells of the rete mucosum Malpighi, as compared with Figs. 2 and 3, due in part to slight obliquity of section. The eleidin and keratohyalin granules of the stratum granulosum not shown. ×750.

of pathologically pigmented skin; also a melanotic sarcoma, several pieces of pigmented skin of incomplete history, sections of infant's scalp and eyelid of newborn mulatto. Individuals were classified as blond or brunet according to color of hair. Mulattos were so adjudged in most cases from general appearance, *i. e.*, absence of distinct negro features, *e. g.*, thick lips, flat nose, etc., though in several cases the individual con-

tributing the skin admitted to me being "mixed." All but one piece of mulatto skin were tested by the Bradley color top before embedding. In only one case (No. 2) could the individual contributing negro skin be questioned by myself in regard to purity; the remaining four pieces are so classified on the assurance of pathologist and surgeon. Four pieces were tested with the color top. Sections were cut both in celloidin and paraffin, and studied unstained and stained (with 1/12 oil immersion lens) in carbol fuchsin or the hematoxylin and eosin combination. The following is a list of the specimens and the essential points of interest regarding each:

FIG. 2. Drawing of section of light brown mulatto skin (specimen No. 3) showing distribution of the pigment granules in the rete mucosum Malpighi. Darker and lighter mulatto skins differ from this only in the greater and smaller number, respectively, of melanin granules. ×750.

1. Pure negro; from postmortem by Dr. H. Marshall (professor of pathology, University of Virginia); Zenker's fixation; color (matched by mixing yellow, white, red and black on the Bradley color top)—yellow, 4 per cent.; white, 8 per cent.; red, 22 per cent.; black, 66 per cent.

2. Pure negro woman; from abdominal operation by Dr. Harvey Stone (adjunct professor of surgery); fixed in 95 per cent. alcohol; a shade lighter than No. 1.

3. Light mulatto woman; abdominal operation by Dr. Stone; 95 per cent. alcohol fixation; color—yellow, 10 per cent.; white, 18 per cent.; red, 22 per cent.; black, 50 per cent. (Fig. 2).

4. Light mulatto; abdominal operation by Dr. Stone; 95 per cent. alcohol fixation; a shade darker than No. 3.

5. Blond; abdominal operation by Dr. Stone; 95 per cent. alcohol fixation.

6. Pathologically pigmented (grayish yellow) skin of white individual; postmortem (thyroid adenomata) by Dr. Marshall; 95 per cent. alcohol fixation.

7. Brunet; abdominal operation by Dr. W. H. Goodwin (adjunct professor of surgery); 95 per cent. alcohol fixation.

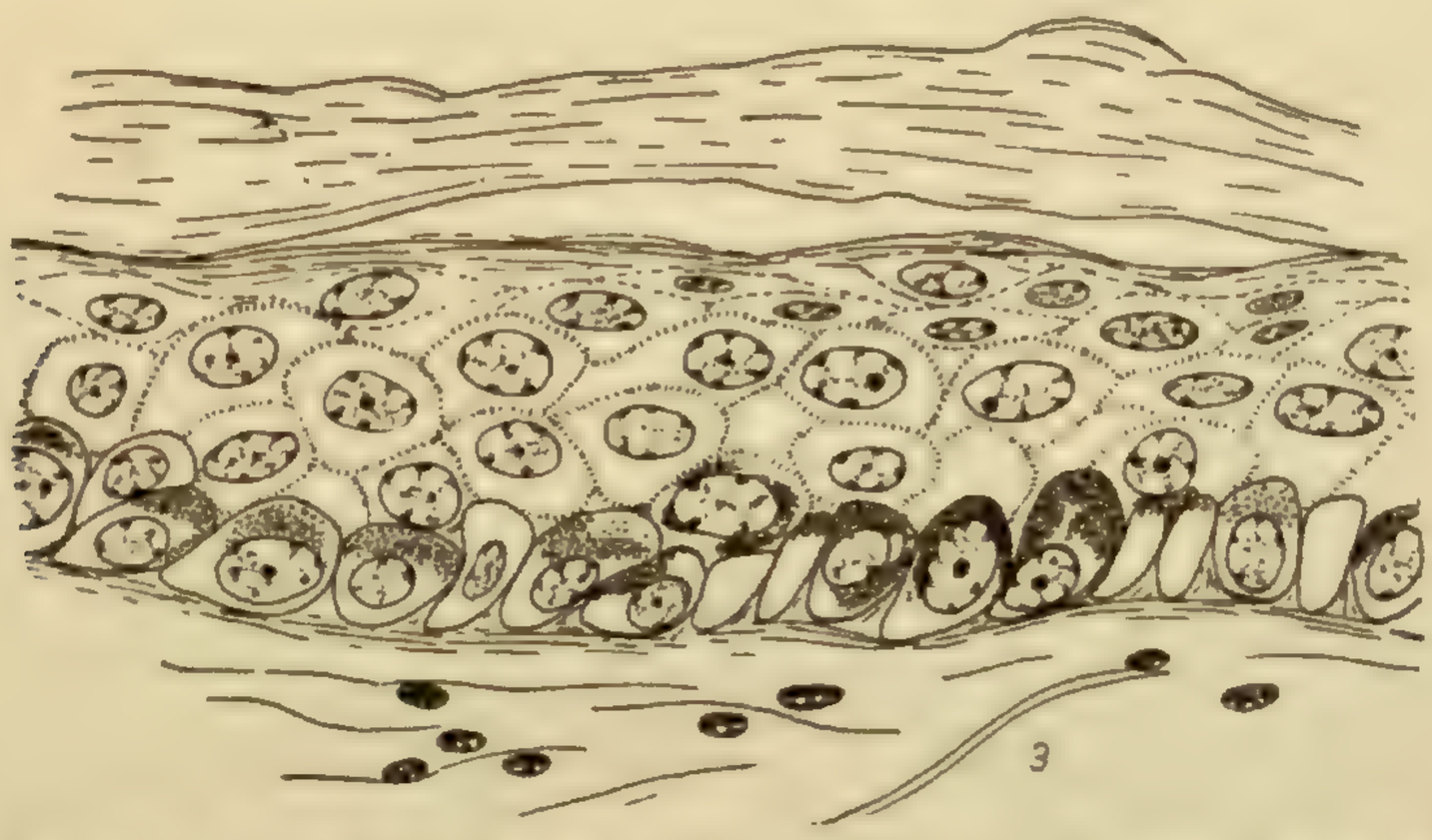

FIG. 3. Drawing of section of skin of blond ("cross between blond and brunet"—specimen No. 13). In lighter blonds (*e. g.*, specimen No. 5) fewer basal cells contain still fewer granules; in darker brunets the basal cells contain more granules. ×750.

8. Light mulatto male (age 80); postmortem (acute cystitis) by Dr. W. Thalhimer (instructor in pathology); Zenker's fixation; color—yellow, 10 per cent.; white, 17 per cent.; red, 30 per cent.; black, 43 per cent.

9. Pure negro; abdominal operation by Dr. Stephen H. Watts (professor of surgery)—95 per cent. alcohol fixation.

10. Brown mulatto boy; abdominal operation by Dr. S. H. Watts; 95 per cent. alcohol fixation.

11. Brunet; abdominal operation by Dr. S. H. Watts; 95 per cent. alcohol fixation.

12. Brunet female (gray); postmortem (goitre and old age) by Dr. W. Thalhimer; Zenker fixation.

13. Dark blond male—age 30 years—("cross between blonde and brunet"); from postmortem (pyæmia and perinephric abscess) by Dr. W. Thalhimer; 95 per cent. alcohol fixation (Fig. 3).

14. Pure negro; abdominal operation by Dr. S. H.

Watts; 95 per cent. alcohol fixation; color—yellow, 5 per cent.; white, 7 per cent.; red, 19 per cent.; black, 69 per cent. (Fig. 1).

15. Pure negro; abdominal operation by Dr. S. H. Watts; 95 per cent. alcohol fixation; slightly lighter than No. 14.

16. Brunet; abdominal operation by Dr. S. H. Watts; 95 per cent. alcohol fixation.

17. Mulatto; abdominal operation by Dr. S. H. Watts; 95 per cent. alcohol fixation; color—yellow, 14 per cent.; white, 14 per cent.; red, 35 per cent.; black, 37 per cent.

18. Mulatto; abdominal operation by Dr. S. H. Watts; 95 per cent. alcohol fixation; a shade lighter than No. 17.

Ranged according to degree of coloration, judged macroscopically, the 17 pieces of skin (omitting No. 6) take the following order:

Negro *9*, *14* (B, 69), *1* (B, 66), *2*, *15*.

Mulatto *4*, *3* (B, 50), *8* (B, 43), *17* (B, 37), *10*, *18*.

Brunet *7*, *11*, *12*, *16*, Blond *13*, *5*.

This list could have been enlarged indefinitely, but more material was not deemed requisite to the demands of this study. Number 6 took rank between numbers 18 and 7.

Sources of Epidermal Pigment.—There are obviously three distinct views which might be held—and as a matter of fact have been held—in regard to the origin of the pigment of the skin: (1) In the epithelial cells of epidermis; (2) in the connective tissue cells of the dermis, and secondarily transferred to the cells of the rete mucosum Malpighi; (3) in both the epithelial and connective tissue cells. The second view more especially further involves the question as to whether the pigment arises in the connective tissue cells as a result of cellular (secretory) activity or whether the cell extracts the pigment (fully formed or unsynthesized) from the blood; also the manner of the transference of the pigment to the epithelial cell.

There are two works which bear upon this point more directly: (1) That of Karg (1888) who ably supports the second view on the basis of findings from a microscopic

study of white skin transplanted to a negro and *vice versa*, *i. e.*, negro skin transplanted to a white individual; (2) that of Meirowsky (1908), who studied the origin of melanic pigment in the skin and eye and, more especially, on the basis of experiments with pigeons and findings in pigmented skin kept alive for several days in a paraffin bath at a temperature of 56 degrees, urges the first view. These two masterly papers advance diametrically opposing views. Karg unqualifiedly put aside the idea that pigment may be formed within the epidermal cell. He says, "Es gelang so, festzustellen, das es nur eines Modus der Entstehung des Pigments giebt. Aus der Lederhaut dringen pigmentirte Zellen in die Epidermis, verästeln sich hier weit und geben ihr Pigment an die Epithelzellen ab," p. 370. Meirowsky describes conditions more in conformity with our later ideas of cellular physiology. According to him, the melanic granules are passed out of the nucleus of the epidermal cell into its cytoplasm, *i. e.*, pigmentation is an intracellular process, both dermal and epidermal.

Historically Riehl (1884) appears to have been the first to describe the condition afterwards interpreted by Karg as supporting his view of epithelial pigmentation, viz., invasion of processes of pigmented connective tissue cells among the epidermal cells. Riehl studied more especially the pigment of hair. He did not generalize, however; and while he thought it improbable, he did not regard it impossible, that pigment may arise out of the protoplasm of epithelial cells. He seems rather to incline to the third view above stated. Moreover, on the basis of findings in a study of three cases of Addison's disease, where the adventitia of blood vessels was richly infiltrated with pigmented cells coincidentally with a hemorrhagic aggregation of red blood cells, he concludes that the pigment arises from the hæmoglobin of the red cells. Aeby (1885) likewise describes the transportation of pigment to the epidermis by wandering cells. Ehrmann (1885–86), who studied the pigmented epithelium of amphibia, differs from Riehl and Aeby only in holding that the pigmented stellate cells of the cutis

are non-motile. He describes a network of pigmented cutis cells (chromatophores) connected with the epidermis by processes through which the pigment granules stream into the epithelial cells of the rete mucosum Malpighi. He also concludes that the pigment arises from the hæmoglobin of the red cells, since the pigment cells are most abundant in the vicinity of the blood vessels. The reception of the pigment granules by the epithelial cells he regards a phagocytic process, the epithelial cells being described as corroding the processes and assimilating the contents as part of their own organization. The important observations of Jager (1885) on pigment spots in dog and rabbit after inflammation, and those of R. Krause (1888) on apes, are in substantial accord with those of the afore-mentioned investigators, more particularly in regard to the secondary origin of pigment in the epidermis, and the primary source of the same in the blood. For further information regarding literature of pigment cells, more particularly in the lower vertebrates, the reader is referred to the splendid article by Karg.

It remains to outline more fully Karg's position as representative of the second view above stated. Pigmentation of epidermis and its appendages (hair, etc.) is a secondary process. The pigment is transferred to the epithelial cells through cells which have their origin in the cutis (*i. e.*, chromatophore, Ehrmann). They wander into, or, remaining on border line between epidermis and cutis, send processes into the intercellular spaces of the epidermis. They end in the epithelial cells (capable of a certain amount of amœboid motility) to which they surrender their pigment through process of absorption causing streaming from process to cell. These pigmented cells are wandering cells of the nature of connective tissue cells. They are thought to obtain their pigment from the blood. This, however, is not regarded as hæmoglobin since no red corpuscles are ever seen in these cells. There is here (*i. e.*, in transplanted human skin) no network of pigment cells as described by Ehrmann in amphibia. Nor can the pigment cells be

pigmented leucocytes since they have no similarity to the latter, nor are pigmented leucocytes found in negro blood. In the cutis he claims to be able to see all the transition stages between pigment-free connective tissue cells and such as are strongly pigmented. On the basis of his findings he thinks it appears only reasonable that in the pigmenting skin (transplanted white) the earlier unpigmented granules (Reinke's trophoplasts; Altmann's bioblasts) of the chromatophore take on a dark color (by as yet unknown ways) and that this is connected with the presence of blood; and that it can not, however, be regarded as the product of fragmentated red corpuscles. Melanin may be hemosiderin, but is the product of a living cell. His final position thus approaches somewhat to Meirowsky's, though they still differ as to the cell that elaborates the pigment for the epidermis. It is important in this connection to note that while Karg describes numerous branching pigmented connective tissue cells (wandering cells) among the epidermal cells of the transplanted white skin, he failed to find such in the normal skin of the negro. He thinks it probable that such may be found in the skin of the negro embryo.

Meirowsky in his monograph also gives a very complete review of the literature to date. He uses experimental methods mainly. His findings supporting the first view may be briefly summarized: Pigmentation is possible in the epidermis without the agency of "melanoblasts," or even any aid from the cutis. There are both epidermal and cutis melanoblasts, and they are independent of each other. Pigmented epidermal cells are capable, under certain stimuli, to assume irregularly branching forms (filling the intercellular spaces) simulating mesodermal chromatophores (so-called melanoblasts) which might have wandered into the epidermis. This is probably the correct interpretation of Karg's figures. He brings forth cytological evidence to show that the pigment arises from a reddish nuclear substance (a "pyroniuroter Kernsubstanz")—he does not commit himself as to its chemical nature—which passes into the cytoplasm and gradually assumes the yellowish

brown color of the melanic granules. These results from experimental procedure are confirmed by findings in the retina of the calf embryo, where the identical stages in pigment formation are observed. He thinks it more probable that the pigment has origin in an albuminous substance (this is in complete accord with the work of Chittenden and Albro—1903) of the nucleus than that hæmoglobin has any contributory rôle. The earlier stages in such a process can be observed in carcinoma without progress to the final stage of pigmentation. This indicates that we are probably dealing with a nuclear substance, which, shed into the cytoplasm, under the influence of an oxidation enzyme, becomes a melanic substance.

As bearing on the point of the origin of pigment my own observations are as follows: No undoubted branching pigmented cells can be seen among the colored epidermal cells in any of my specimens. Occasionally a process of a pigmented connective tissue cell of the cutis is seen to extend for some distance into the rete mucosum Malpighi (Fig. 1). But their number seems very much too meager to supply the pigment of the many colored cells of the epidermis. There is a nice correspondence between the relative abundance of pigmented cells in the dermis and epidermis of the several specimens of skin. In light skins there are few of each type in each layer; in darker skins there is a decided increase in both. But this proportional increase is as reasonably interpreted as due to the same cause influencing both layers, as that the increased number of pigmented epidermal cells demands an increased number of cutis melanoblasts. Moreover, when one considers that there is a continual exfoliation of the superficial layers and a replacing of the same from the lower layers, the number of epidermal pigmented cells in colored skins seems out of all proportion to the number of the cutis melanoblasts which are supposed to furnish the pigment.

The pigment cells of the cutis are most abundant along the border between dermis and epidermis and along the capillaries of the vascular papillæ. This first point would seem to indicate the function ascribed to them by Karg

and others, but when one assumes (as all investigators agree in doing) that pigment formation is somehow related to the blood as source of nutrition or supply, the segregation of the pigmented cutis cells at this level becomes intelligible on other grounds, *i. e.*, necessary closeness to the capillaries of papillæ. Only those layers of the epidermis next the border line (*i. e.*, next the capillaries) have the pigment granules of the prevailing size and color for normal pigment cells. Thus my evidence points to a dependence of both cutis and epidermal cells upon the same source (the blood of the capillaries) for a sine qua non of pigment formation, and an independence of each with respect to the other as a necessary source of supply or even as an aid to pigmentation. That the blood constituent is not hæmoglobin the arguments of Karg and the observations of Meirowsky seem conclusively to prove. That it is not an iron-containing element (*e. g.*, hæmosiderin) I have demonstrated by the method of testing with potassium ferricyanide as used by Brown (1910) for the liver. Chemical analysis by Abel and Davis (1896) also has shown that the melanic pigment of the hair and skin of the negro is free of iron. The evidence at hand, as furnished by Chittenden and Albro, von Fürth, Spiegler, Gessard, Riddle, Meirowsky, and others seems to render it very probable that in vital melanogenesis we are dealing with a proteid substance (tyrosin; trophoplast; chromogen) acted upon by an enzyme or oxidase (tyrosinase) and that one (probably the former) is supplied by the cell (nucleus) and the other by the blood.

The fact that the pigment granules, in epidermal cells that are not packed with them, are segregated in the distal portion, indicates that they are responsive to the influence of light. However, the further discussion will not be complicated by a consideration of this possible factor. The following discussion will accept as well supported the position that pigment is formed in the epidermal cells—the analogous formation of pigment in ganglion cells gives further support—by virtue of a cellular metab-

olism made possible by close association with the nutritive source, *i. e.*, blood vessels.[1]

[1] A specimen of leucoderma from a dark negro obtained at autopsy through the kindness of Dr. W. Thalhimer gives further evidence in support of this position. Macroscopically, the two leucodermic areas, about 5 cm. in diameter, and bilaterally symmetrically placed over the clavicles, appeared perfectly normal except for their very much lighter color (grayish yellow). A section through the transition area shows the following histologic conditions: (1) The leucodermic area contains a comparatively very large number of pigmented cells in the corium. (2) In the epidermis the comparatively small amount of pigment present is confined to some of the columnar cells of the stratum Malpighi. (3) The corium of the pigmented skin has only a moderate amount of pigmented cells. (4) In the epidermis of the normal skin, the columnar cells are laden with melanic granules, and all of the more superficial layers of cells contain a considerable amount of melanic pigment. (5) The pigment granules are everywhere the same in respect to color and size. (6) The epidermal cells appear identical, except for the variable abundance of the pigment granules, in the two regions. In view of the above facts, it seems clear that lack of pigment in the epidermis of the leucodermic patch is not due to a dermal deficiency (supposing the derma to be its source of supply), nor to an inability on the part of the epidermal cells to take up pigment (since they harbor a small amount). These facts speak in favor of the epidermal origin of the epidermal pigment, and indicate a local inability on the part of the epidermal cells to manufacture in normal quantity (for this individual) the melanic granules. Furthermore, interpreting melanogenesis in terms of tyrosin and tyrosinase, the facts indicate a local deficiency or inhibition of one of these factors. It seems more reasonable to suppose that the columnar cells of the epidermis of the leucodermic areas were for some obscure cause (nervous?) unable to elaborate the granules (''pyroninroter Kernsubstanz,'' Meirowsky) which, under the influence of an oxidase probably everywhere present, turn melanic.

The recent work of Dyson (''An Investigation on Cutaneous Pigmentation in Normal and Pathological Conditions,'' *Journ. Path. and Bact.*, 15: 3, 1911) in the main also confirms Meirowsky's findings regarding the nuclear origin of the melanic granules in the epidermis of pigmented skins (after treatment with the Finsen lamp). Dyson describes ''blue granules which owe their staining capacity (in hæmatoxylin) after bichromating to the presence of an unsaturated fatty substance.'' very similar to the ''pyronin-red substance'' of Meirowsky. These granules Dyson regards as ''the mother substance of pigment. These granules are complex in character, being composed of a lipoid and proteid element: the proteid portion precipitates out after its escape from the nucleus and remains as a foreign body in the cytoplasm of the cell; whilst the larger granules seen at the periphery of the cells I regard as the lipoid substance after the separation has taken place; these granules then escape into the intercellular lymph spaces'' (p. 314). The ''pyronin-red'' substance he interprets as ''probably the chromatic proteid portion of the complex granules from which the lipoid portion has been dissolved by his (Meirowsky) method of preparing his material,'' *i. e.*, use of alcohol (p. 316). In origin melanotic pigment is then a lipochrome, the melanin being the chromatic proteid portion after

Cause of Degree of Coloration.—Theoretically at least six possibilities are conceivable: (1) Number of pigmented epidermal cells, or, indirectly, (2) number of pigmented connective tissue cells of cutis, (3) number of pigment granules in pigmented epidermal cell, (4) coloration of granules in pigmented epidermal cells, (5) numbers 1 and 3, (6) combination of 1 or 3 and 4, or a combination of the three. It is also theoretically possible that a difference in the size of the granules may play a part in determining the degree of coloration. In view of what was said under the previous heading, number 2 can be disregarded and there remain five plausible possibilities. Which "possibility" or set of possibilities expresses the reality will become clear from the description of the several types of skin. In anticipation of ensuing results it may be said in brief that there seems to be only one factor in skin coloration, viz., the number of the pigment granules, a greater number of granules of course involving a greater number of cells—with a small and possibly negligible variation in size.

DESCRIPTION OF NEGRO SKINS

The several samples of skin will be described in the order of their degree of coloration as seen from the surface. This agrees almost absolutely with the degree (*i. e.*, quantity) of the pigmentation factor, as will appear below.

its separation from the complex lipoid granules. In several points my findings in leucoderma do not accord with those of Dyson: (1) While it may be true that the pigment granules of the cutis cells are slightly coarser, I can not regard them as darker than those of the epidermis. (2) In no case have I been able to discern melanic granules in the nuclei (studied in *unstained* preparations). (3) I find a greater relative amount of cutis pigment in the specimen of leucoderma, whereas Dyson reports no pigment in the cutis of his two samples of leucoderma. (4) Consequently (and for still other reasons) I can not accept his position that cutis pigment is secondary to epithelial, *i. e.*, that pigment passes from epidermis via lymph channels to the derma where it is supposed to be taken up by wandering cells. If this were true the cutis underlying the more highly pigmented epithelium should contain relatively (to leucodermic area) more pigment. But just the reverse is the case in my specimen. In fact the amount of pigment in the epidermis would seem to be too meager to supply the cutis pigment present under the leucodermic patch. All the evidence indicates that the path of pigment transportation is from depth to surface of epidermis.

All the samples being taken from the same body region, there is a very close correspondence in the number of epidermal layers involved.

Number 9: Here all the epidermal strata of cells are pigmented. In the basal layer the cells are packed with the yellowish brown spherical granules to such an extent as partially to obscure the nucleus and cause the cell to bulge. In the more superficial layers, the granules are massed distally and more scattered proximally, the nucleus appearing very prominently. In the cutis, chromatophores are abundant, their granules being similar in shape, size and color to those of the basal epidermal layer. These cells are always in the near vicinity of the blood vessels. In the upper layers of the epidermis the pigment granules become darker, finer and frequently of oblong shape. These several differential features are ascribed to the several factors of desiccation, pressure and keratization that the containing cells undergo in their passage to the exfoliating surface. The same explanation probably (at least to some degree) applies to the invariably darker bacillary pigment granules of the shaft of the hairs appearing in all of the sections of this first group.[2] In sections of child's scalp, however, both shaft and bulb contain the same yellowish-brown granules as found in the skin, the only appreciable difference being a considerable irregularity in shape and size. It must be noted here that not all the basal cells (though in negro skin the exceptions both in dermis and epidermis are rare) are equally packed with granules. The optical effect of a small number of granules is a lighter shade of brown than that given by a denser mass of identically colored granules.

The objection may be raised that discrimination or lack of discrimination between a darker and lighter pigmented granule is the result of an interpretation where the " personal equation " may factor largely. It is not denied that it is difficult to satisfy oneself absolutely that the granules

[2] I have recently found a very striking exception to the usual brown color of melanic pigment under ordinary conditions in certain cells of young turtles (ca. 25 mm. stage of development). Here growing and dividing cells of the choroid, epidermis, connective tissue generally, and bone marrow contain absolutely black pigment granules.

of the various basal cells of the same and different samples of skin are of identically the same color (the color difference between the skin pigment granules and those of the sections of attached hair is decided enough) but all possible caution was observed to offset the personal factor. In short, when the writer after much study was still somewhat undecided as to a definite stand, the slides were shown to three different professors, all with long training and much experience in the use of the microscope. These men were asked to answer the following questions with respect to the basal cells of the eighteen samples, and this without knowledge of what the other men had written: Are the pigment granules of the samples of skin of the same color or of different colors? Name the color or colors? The replies were uniform in recognizing only one type of granules, and in describing it as "yellowish brown," "brownish yellow" and "a dark golden or yellowish brown—amber—somewhere between brass and copper," respectively. One man noted the slightly darker shade of the granules of the more superficial cells.

Number 14 (Fig. 1): All the layers are again pigmented, but there is a slightly smaller amount in the upper layers than in number 9. The pigment cells of the cutis are here somewhat more numerous, showing many anastomosing processes, and forming in places a network of pigmented strands just beneath the scarf skin. A variation in amount of pigment in different regions of the basal layer is again evident. The deeper color of number 9 as compared with 14 seems due to the greater amount of pigment present in the superficial layers.

Numbers 1 and 2 are very like the foregoing except that there is a slight decrease in the number of greatly packed basal cells.

Number 15: This sample shows a quite appreciably smaller number of pigment cells in the epidermis and a yet more pronounced decrease in the corium.

DESCRIPTION OF MULATTO SKINS

Number 4: The number of granules in the great majority of the basal cells of the epidermis is somewhat less

than in the last of the foregoing group. Cells also now appear in the lower layers with only relatively scattered granules. There is an almost complete absence of granules from the cells of the superficial layers. There are decidedly fewer pigmented cutis cells. Hair in section again shows the same sort of pigment granules as above described. This statement holds good for hair wherever they have appeared in these sections (not seen in the samples of blond skin).

Number 3 (Fig. 2): The pigmented basal cells of this specimen contain still fewer granules than in number 4. The very small number and size of the chromatophores of the corium is striking. Here again only the cells of the rete mucosum Malpighi contain the granules.

Number 8 is almost identical with number 3.

Number 17 is like number 8 with slightly less pigment in the rete mucosum Malpighi; but here the superficial layers again contain a considerable quantity of melanin granules and the melanic cutis cells are more abundant than in numbers 3 and 18.

Numbers 10 and 18 are both very like number 8, showing only a slight decrease in the quantity of pigment.

This seems the best place for a brief discussion of the foregoing facts. What is the fundamental cause of the difference in the degree of color of the skins described? Plainly, I believe, a difference in the abundance of the pigment granules in the basal cells of the rete mucosum Malpighi. A densely packed mother cell of this layer gives rise to two daughter cells of very similar constitution which are only slightly altered as they pass to the upper layers. Hence in skins where the basal cells manufacture much pigment, the entire rete mucosum Malpighi, formed of its descendants—the factors of desiccation and cornification not being able at once to produce a very appreciable destruction or modification of the granules—will appear pigmented. But between negro and mulatto skin there does not seem to be any apparent difference as to the number of epidermal cells producing pigment, but only as to the quantity of pigment produced by the same basal cells, an initial greater quantity determining a secondarily persisting greater quantity, and thus an apparently greater num-

ber of epidermal pigmented cells. Probably also, the cells generally of the rete mucosum Malpighi retain in small degree the property of the basal mother cell to produce pigment granules.

DESCRIPTION OF SKIN OF BRUNET

Number 6 (pathologically pigmented skin) : Here one is unable to determine just how much pigment is due to the normal (" midway between blond and brunet ") and how much to the pathologic condition ("thyroid adenomata" —"gall stones, but not jaundiced"). The specimen contains fewer granules than number 18 and more than number 7.

Number 7 : Here the granules are very few in number and confined exclusively to the basal layer. There is great variation in the number of granules held by the basal cells. Only very rarely does a small pigmented cutis cell appear in the sections.

Number 11 has still fewer granules than 7 and

Number 17 shows only occasional cells of the basal layer slightly pigmented (few melanin granules).

Number 16 is more like the blond skin to be described. There are very few granules in only occasional cells; and no pigmented cutis cells are seen in the section. This skin could not be told from blond.

DESCRIPTION OF BLOND SKIN

Number 13 (Fig. 3) : Here the layer of distinctly pigmented basal cells is fairly complete. The section is very like number 7 of the brunet series.

Number 5 is almost identical with number 16. The pigment granules are very rare; and only a few to a cell.

It must be emphasized at this point that the melanic granules of number 5 are in point of shape, size and coloration indistinguishable from those of number 9.

There is a continuous gradation in color (and the number of pigment granules) from negro to blond skin with an overlapping at the extremes.

The melanic granules of the specimen of melanotic sarcoma were of the same yellowish-brown color (perhaps of a trifle lighter shade), but of very irregular shape and

with great variations in size (the larger "granules" may be the result of fusion of smaller masses).

Statement of Results and Related Facts

The facts whose interpretation is sought in terms of some principle of heredity are these: (1) The degree of skin coloration is due to the variable number of pigment granules in the cells of the rete mucosum Malpighi involving incidentally a variable number of more superficial cells. (2) The pigment granules (melanic) of all skin (albinos excepted) are identical in size (practically), shape and color (without qualification). (3) The ascending scale of morphological conditions paralleling a progressively deepening grade of pigmentation may be described as follows: (*a*) few cells of basal layer pigmented with few granules—blonds, (*b*) more cells containing more granules—brunets, (*c*) a more or less complete basal layer of cells with many and very many melanic granules (mulattos), (*d*) the cells of basal layer packed and distended with pigment granules; the cells of the more superficial layer also with very many granules.

Or, restated and explained, (4) The progressive increase in progressively darker skins both in the number of granules and in the number of the pigmented cells. That these two facts are related to each other as cause (number of granules) and effect (number of pigment cells) is strongly indicated by the fact that in light mulatto and brunet skins, where only the basal cells are distinctly pigmented, the number of granules per cell in general decreases with the progressively lighter shades.

(5) The results recently published by the Davenports showing a segregation of the original skin colors (grandparental colors) among the individuals of the third generation, *i. e.*, children of mulatto parents.

(6) The accumulation of the pigmented cells near the border line between the dermis and epidermis or in the vicinity of the blood stream.

(7) Melanin formation is an intracellular metabolic process going on independently and in a measure proportionately in both dermis and epidermis. This seems demonstrated by the researches of Meirowsky and others,

and the view is indirectly supported by the comparative findings above described, viz.: (*a*) absence of connective tissue cells (chromatophores) among the epidermal cells (admitted by Karg for normal negro skin), (*b*) comparative rarity of pigmented processes from cutis cells, and (*c*) an apparently disproportionate number of chromatophores as compared with the epidermal pigment cells.

(8) The agreement between the cytologic facts of Meirowsky and the chemical results of Chittenden and Albro, and others, that the antecedent of melanin is some form of proteid.

(9) The observations of Meirowsky showing a passage of granules from the nucleus to the cytoplasm as the initial step in melanogenesis, and a progressive coloration of these granules to a final stage of yellowish-brown pigment.

(10) The production of artificial melanins ("melanoidins"—Schmiedeberg) by Chittenden and Albro and others from "antialbumid" and various proteids, and the results described by Spiegler and Riddle and others indicating an interaction of a chromogen (tyrosin compound) with an oxidizing enzyme (tyrosinase) in the formation of melanin.

DISCUSSION

There appears, then, proximately to be only one factor in skin-pigmentation, viz., the number of granules of identical shade (yellowish-brown), incidentally the number of cells containing such granules. The granules would seem to be the result of intracellular activities (Meirowsky) and to have origin in cell proteids (Chittenden and Albro, and Meirowsky). In terms of chromogen and oxidase, the granules may be thought of as tyrosin which under the influence of tyrosinase from the blood or tissues generally becomes melanic.

The melanogenetic process seems to stop at the same point in all grades of colored skin, from negro to blond—in hair of the same it may possibly proceed slightly further, though even this seems doubtful in view of appearances in the hair bulb. One seems to be dealing, then, with a continuous process, *i. e.*, the production of melanic

granules; and the numerical point at which the process stops determines the color of the skin. But thought of in terms of greater and lesser ability for tyrosin production (intervention of a tyrosinase-producing factor would modify the results, but not fundamentally alter the mechanism of inheritance); and attributing such factor to a specific cell-organ which may be a chromosome or part of such ("teleomorph"—Spillman), the segregation noted by the Davenports becomes as intelligible as other Mendelian phenomena. From the standpoint of the number of granules some mulatto skins are certainly different from a "blend" between negro and white, and this is true in the direction both of more and of less—from the standpoint of the amount of pigment some mulattos are identical, on the one hand, with negros and on the other with brunets—and evidences a measure of segregation of "strong melanogenesis" and "slight melanogenesis."

A plausible interpretation of Karg's experimental findings might be made on the basis of a larger and smaller amount of tyrosinase in negro and white blood, respectively—or more likely perhaps on the basis of more and less pronounced stimulation by negro and white blood, respectively, to tyrosin production.

The occurrence of melanotic sarcomata in albinos and white horses forces the assumption that in both cases tyrosinase is present, as in ordinary colored animals. In albinos there is evidently an absence generally of tyrosin in usual events (production of tyrosin locally accords better with our present knowledge than a hypothesis of local tyrosinase production). If Spiegler's view represents the veritable condition, viz., that in white horses there is present a white melanin—rendered quite doubtful by Gortner's recent work—the end-result of an oxidation process of tyrosin, the presence of melanotic tumors in white horses may be explained in the same way as in ordinary cases, as shown by the work of Gessard.

Accordingly, when one considers the question of color inheritance among crosses between ordinary white individuals and albinos, two factors (at least—these most prominent and apparently most important; a "multiplicity of units" or factors may be involved in color-in-

heritance as the Davenports suggest) appear to be involved, *i. e.*, a tyrosin-producing factor and a tyrosinase-producing factor, one at least a function of the epidermal cell, and both having as likely a chromosomal representative (a "teleomorph"—Spillman) as any other cell organ or function. The tyrosin-producing factor is probably generally absent in albinos, locally appearing abnormally in tumor cells, hence two albinos can never produce colored offspring, as amply shown by the results of the experimental breeders.

The observations of Stedman, reported by Bateson (p. 227) "to the effect that an albino negress married to a European had children all mulattos" does not necessarily imply that the factor determining the blackness of the negro (tyrosin production) was carried by the albino. Mulattos are frequently so classified on the basis of marks other than color of skin. Many mulattos are no darker than many white brunets. In the above case the factor controlling tyrosin production may very well have been contributed by the father alone. This instance does not necessarily controvert the assumption that albinos lack the factor of tyrosin production.

Moreover, crosses between albinos and pigmented individuals result in families where albinism greatly preponderates, as shown in the recent "dissertation" by Stainer. In crosses between whites and blacks one deals apparently more especially with the factors of great and small capacity for tyrosin production—tyrosinase being probably of more general distribution. Judging from the pedigrees published by Stainer, absence of capacity for tyrosin production (albinism) in man behaves more like a dominant character (or at any rate, not like a pure recessive) to the presence of such capacity. This is not in accord with the results of the Davenports, which seem to indicate that "internal conditions that lead to deeper pigmentation dominate over the weaker conditions"; similarly as regards color of hair and eyes, "the more pigmented condition tends to be dominant over the less pigmented" according to the earlier investigations of Holmes and Loomis as well as the more recent work of the Davenports. Nor does it accord with the results of

the experimental breeders with lower mammals. It may, of course, be found that all mammalian albinos have the white pigment (melanin) described by Spiegler for white horses. Such a result would seem to correlate a number of apparently discordant facts. It would obviate the further assumption of an "antioxidase" suggested by Gortner, and render more intelligible the non-recessive behavior of human albinism.[3] No theory of color-inheritance is satisfactory that can not embrace all the facts of albinism, and such is the present state of affairs.

In crosses between whites and negroes there is generally a partial dominance of the deeper pigmented condition over the lighter in the second (mulatto) generation; the third generation showing a measure of segregation of the original colors. The partiality and incompleteness of dominance and segregation may be due to a "myriad" other factors modifying and obscuring more or less the final results.[4]

Seeing that we are dealing with only one kind of colored granules, the apparent segregation noted in the families of mulatto parents does not here seem to be due to a condition of unstable equilibrium in the chemical constitutions of the parental melanin and an attempt at readjustment to an original state of greater stability, as suggested by Riddle.

The apparent continuity of the melanogenetic process, as seen in the continuous numerical gradation of the same colored pigment granules where a graded series of skins is examined, rests, in fact, where single families of mulattos are considered, upon discontinuities or discrete

[3] In the second part of Davenport's paper on "Heredity of Skin Pigmentation in Man" (AM. NAT., Vol. 44, No. 528) is presented an array of facts, drawn from a study of a large number of albino families, that furnishes the most cogent argument yet offered for the recessive nature of albinism.

[4] Professor L. W. Lyde, in an article on "Climate and Racial Skin Color" (*Contemporary Review*, February, 1911), states his conclusion that "pigment is latent in all humans and depends for its development on relative action of the lungs and intestines, which is in turn decided by sunlight and humidity." On the other hand, Professor J. H. F. Kohlbougge ("The Influence of a Tropical Climate on Europeans," *Eugenics Review*, April, 1911) believes that "there is no reason for assuming that a dark complexion is due to climate."

"unit characters" controlling conditions of a more and a less numerous production of melanic granules, which conditions conform more or less closely to an alternative mode of inheritance.

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A COEFFICIENT OF INDIVIDUAL PREPOTENCY FOR STUDENTS OF HEREDITY

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I. THE CONCEPTION OF PREPOTENCY

THE term prepotency conveys the general idea that certain individuals "are particularly apt to impress their personal characters upon their offspring." Like most terms of general biology it has been applied in several different connections. The much-needed threshing over of the literature to separate the few measures of wheat from the stacks of straw and weeds falls outside the scope of this note.

One may follow Vilmorin, Hallett, Hays and many other noted breeders in the recognition of the practical importance of the fact that two individuals may be externally exactly alike and yet produce quite dissimilar offspring, without pledging himself to any of the theories of heredity in support of which it is sometimes cited. The aim of the practical breeder is not to formulate or to test theories of heredity but to get a strain of wheat which will draw the maximum amount of flour from an acre of soil or a breed of beasts that will yield the largest net dividends in milk, eggs or steak. His problem is preeminently a practical one, and one of the greatest services the student of biology can render him is to provide the criteria which enable him to select as easily as possible the parents of a race which will meet his requirements.

The purpose of this note is to call the attention of students of heredity to certain formulæ[1] which may be of

[1] These formulæ have heretofore been used in anthropometric surveys in testing the divergence of the inhabitants of a restricted community from the population of the whole area under consideration. They are equally

service in estimating the desirability of individual parents.

By individual prepotency[2] we understand for present purposes the phenomenon of certain individuals, or pairs of individuals in bi-parental inheritance, being exceptional in their capacity for producing offspring of any given characteristic.

As used here the term prepotency is most general. It implies nothing concerning the somatic similarity[3] of parent and offspring and is in no way dependent upon any theory of heredity. It merely expresses a fact well known to practical breeders for half a century.

By a coefficient of individual prepotency one understands a statistical constant which measures the degree of superiority (with respect to the capacity for the production of offspring of any desired type) of any single parent or pair of parents.

well adapted to determine the significance of the deviation of an individual family from its generation.

The fundamental papers are:

Pearson, K., "On some Properties of the Hypergeometrical Series, and on the Fitting of such Series to Observation Polygons in the Theory of Chance," *Phil. Mag.*, February, 1899, p. 239.

Pearson, K., "On the Curves which are most Suitable for Describing the Frequency of Random Samples of a Population," *Biometrika*, Vol. V, pp. 172–175, 1906.

Pearson, K., "Note on the Significant or Non-significant Character of a Sub-sample drawn from a Sample," *Biometrika*, Vol. V, pp. 181–183, 1906.

Pearson, K., "On a Coefficient of Class Heterogeneity or Divergence," *Biometrika*, Vol. V, pp. 198–203, 1906.

Tocher, J. F., "The Anthropometric Characteristics of the Inmates of Asylums in Scotland," *Biometrika*, Vol. V, pp. 315–318, 1907.

Tocher, J. F., "Pigmentation Survey of School Children in Scotland," *Biometrika*, Vol. VI, pp. 143–146, 162–164.

[2] The disadvantages of using a word which has been so variously employed as prepotency are offset by keeping the terminology as simple as possible. The important thing is to have all terms carefully defined and unambiguous wherever used.

[3] In any study of heredity the correlation between the somatic characters of the parents and their offspring must be taken into account. Prepotency may, however, be estimated solely from the germinal characters of the parents as expressed in their respective arrays of offspring.

II. The Measurement of Individual Prepotency

However well one may know the somatic characters of an individual or however intimate his knowledge of its ancestry the ultimate test of its value as a starting point for a new race is the quality of its offspring. *The proof of the parent is its produce* has been recognized as valid by various breeders since the time of Louis Vilmorin, who separated the parent beets and judged them individually by their offspring. The "ear-to-row" test in corn breeding, Petkus von Lochow's row-tests in rye and Hays's "centgener power" all represent attempts by practical breeders to obtain measures of individual prepotency as the term is used here. Galton's study of the distribution of prepotency in horses falls in the same class.

The method of estimating prepotency directly from the mean value (*e. g.*, sugar content) of the offspring, or from the number of offspring surpassing a given standard (*e. g.*, a mile in 2:30, or better, on the track) has distinct advantages which will be obvious to those acquainted with elementary statistics.

So far as I am aware the credit of first recognizing the need of taking into account both type and variability in the criterion by which the relative desirability of the individual parents should be judged is due to Waugh.

In discussing some results secured on experiments with peas he remarks:[4]

> . . . There were, as always, some exceptional cases of individual vines which showed a marked ability to transmit their individual characters to their offspring. The selection of such prepotent plants is evidently an important matter in plant breeding. In order to exhibit this difference we have computed a coefficient of heredity for each parent and for each character under study.

Waugh's formula is

$$C = 1/\sigma D,$$

where

C = coefficient of individual heredity,

σ = standard deviation of offspring,

[4] Ann. Rept. Mass. Ag. Exp. Sta., Vol. 21, p. 172, 1909.

D = difference between numerical value of the parent character and the mean of the same character in the offspring.

In a later report he makes use of this formula "in an attempt to answer the question whether prepotency is inherited or not."[5]

Now while Waugh deserves all credit for suggesting the need of a coefficient of individual prepotency, I think the formula he proposes can not be justified theoretically nor regarded as practically satisfactory.[6]

The requirements of a coefficient of individual prepotency are at least the following:

(*a*) The comparison must be made between the offspring families, not between the individual parent and its offspring.

(*b*) The comparison must be so drawn as to attach importance only to differences significantly greater than the probable errors of random sampling.

(*c*) The coefficient expressing prepotency should be relative, *i. e.*, it should be comparable from character to character.

Proposition (*b*) and (*c*) will be granted without argument. In justification of (*a*) it is only necessary to point out that from the standpoint of the man who wishes to decide which families to continue to propagate and which to burn, the ideal method is one which may be applied to the individuals of any one generation entirely independently of those of any other. Of course this is not to be interpreted as a recommendation that in the routine work of practical or experimental breeding only one generation should be considered. What is meant is that it is desirable to have formulæ which permit of a consideration of prepotency on the data of any (offspring) generation independently. Such a formula does not preclude or render inadvisable the study of many ascendant generations.

[5] Waugh, *loc. cit.*, Vol. 22, pp. 172–175, 1910.

[6] Indeed he himself has pointed out some of the difficulties and has suggested that a better formula might be found.

The necessity of dealing with each generation independently is also imposed by the possibility of a differentiation between any two generations due to purely environmental (meteorological or edaphic) influences. Taken as a whole the entire offspring generation may be superior or inferior to the parental generation; and this because of no hereditary influence of the parents at all, for all families may be raised or lowered proportionally. This fact vitiates at once any comparison between individual parents and individual offspring unless the type and variability of both parental and offspring generation are taken into account.

In the practical work of calculation two cases may be conveniently recognized: in the first, the character is capable of direct measurement on a quantitative scale, in the second, the character is not capable of direct measurement but the individuals may be grouped into satisfactorily defined classes. In the first case the means may be compared; in the second case the proportional frequencies of one class must be used.

(*a*) *Case of Characters Measurable on a Quantitative Scale*

It is well known that the standard deviation of a mean is $\sigma/\sqrt{N}$ and its probable error is .67449 $\sigma/\sqrt{N}$. Given two uncorrelated means m and M, their difference and its probable error is given by

$$m - M \pm .67449 \sqrt{\frac{\sigma^2}{n} + \frac{\Sigma^2}{N}},$$

where σ and Σ and n and N represent the standard deviations and the numbers of individuals involved in the series. Thus it is quite easy to test the significance of differences in means between any two samples, or families in our case. But with a large number of families the labor of a series of such comparisons is prohibitive. What we need is some easily calculated criterion of the biological significance of the deviation of the mean of an

individual family from the mean of the population to which it belongs.

Suppose a population composed of N individuals with a mean of M and a variability of Σ is due to P parents. Now if this population be divided into two random samples of n and N' individuals, m and M' means, and σ and Σ' variabilities the differences in their means will be

$$(m - M') \pm .67449 \sqrt{\frac{\sigma^2}{n} + \frac{\Sigma'^2}{N'}}.$$

But Pearson has shown that the difference between the mean of a sub-sample m which in our case may represent the offspring of a single parent (or pair of parents) and the population mean M is not given by the preceding formula since n is included in N. The formula for such a case as this he has shown to be

$$(m - M) \pm .67449 \sqrt{\frac{\Sigma^2}{N} + \frac{\sigma^2}{n}\left(1 - \frac{2n}{N}\right) - \frac{n(M-m)^2}{N(N-n)}}.$$

This is the formula which we are seeking, the probable error of the difference between the mean for any family and that for the whole population. By calculating $(m - M)/E_{(m-M)}$ for every family we should have a criterion of its superiority or inferiority—the individual prepotency of the parent in question—relative to the average condition in the series to which it belongs.

Tocher has pointed out advantages in using $(m - M)/\sigma_{(m-M)}$ instead of $(m - M)/E_{(m-M)}$, but this is merely a matter of convenience. The significance of the ratios can be tested by tables of the normal curve.

(*b*) *Case of Characters not Measurable on a Quantitative Scale*

For characters not quantitatively measurable two methods of treatment are available. The first consists in testing the divergence of a family from the general population on the basis of the relative frequency of a given character. The second consists in testing the deviation

of a family from the population with respect to the distribution of a character. At present the second of these methods seems of little practical importance for our purpose because of the relatively small numbers of individuals available in breeding experiments, even with plants, and because of the arithmetical routine.

Consider the first method. Let N be the number of individuals in a population due to P parents. Let X be a character common to all but appearing in different intensities (say from 0 development to the greatest possible intensity) in the several individuals, not measurable but capable of division into m classes. Let $s_1, s_2, s_3 \cdots s_m$ be the classes and $y_{s_1}, y_{s_2}, y_{s_3} \cdots y_{s_m}$ be the frequencies in the population as a whole. Now if a single family of n members be observed the probability of an individual belonging to any class, say s_2, is $y_{s_2} / N = p$, while the probability of its not belonging to that class is $(1 - p) = q$. The actual number of individuals with character s_2 in the family should be $np = y'_{s_2}$, while the frequency for the $m - 1$ remaining classes within the family will be given by $y'_{s_1}, y'_{s_2}, y'_{s_3} \cdots y'_{s_m}$ providing (a) that the family is not differentiated from the population, *e. g.*, that there is no individual prepotency in the sense that we have used the term, and (b) that n is so large that the probable errors of random sampling are negligible. In actual work (b) can never, or almost never, be realized. Our problem is to determine whether differences between the theoretical class frequencies, y_s', and the actually observed class frequencies, y_s'', in the family are to be regarded as due to chance merely or whether they are so large that they can reasonably be considered as indicating a differentiation of the family from the population to which it belongs. In short, our problem is to test $(y''_{s_2} - y'_{s_2})$ against its probable error.

Pearson has shown that the standard deviation of $(y_s'' - y_s')$ for any grade is

$$\Sigma(y_s'' - y_s') = \sqrt{npq\left(1 - \frac{n-1}{N-1}\right)}$$

and Tocher has pointed out that as a test for significance of divergence we may use either of the three ratios

$$(a) \qquad (y_s'' - y_s')/\sqrt{npq(N-n)/(N-1)}.$$

$$(b) \quad 100\{(y_s''/n) - p\}/\sqrt{100^2 pq(N-n)/n(N-1)}.$$

$$(c) \quad 100\{(y_s''/y_s') - 1\}/100\sqrt{q(N-n)/np(N-1)}.$$

The significance of these ratios can be judged from the tables of the probability integral.[7]

III. RECAPITULATION

Individual prepotency is here used to designate the superior capacity of certain parents for producing offspring of any desired character. The conception is most general, and does not imply a similarity in soma between parent and offspring, but the prepotency of the parent is judged entirely by the offspring it produces. The term is used merely to describe a long-known phenomenon, and no theoretical explanation is suggested.

Various breeders have tried to obtain a measure of individual prepotency in its present significance. The purpose of the present note is to point out certain biometric formulæ, in use for other purposes for several years, which seem well adapted for this purpose. They at least obviate several of the objectional features of some of the methods which have been employed. Their applicability in practical work will probably be limited by the arithmetical routine, but in experimental studies their importance may be very considerable. Illustration of their application will be published soon.

COLD SPRING HARBOR, N. Y.,
May 19, 1911.

[7] Of course a statistical formula is not applicable to cases not covered by the assumptions on which it was developed. It seems unnecessary to discuss these here. Those using the formulæ should familiarize themselves with the limitations laid down by Pearson and Tocher in proposing the formulæ.

THE ADAPTATIONS OF THE PRIMATES

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THE development of the primates has taken place in regions of comparatively high temperatures, especially in tropical and semitropical climate. This is chiefly due to their arboreal adaptation, which keeps them where the trees throughout the year offer food either as fruit, leaves, blossoms, insects or small animals.

The first primates are yet to be found, but they doubtless lived either during the last of the Cretaceous or in the earliest Eocene; for during the Lower Eocene of the Wasatch epoch there suddenly appear in America two well-distinguished families of primates, the general feeders or Notharctidæ, and the fruit eaters or Anaptomorphidæ.[1] Between these no intermediate or ancestral group is known, but the wide divergence in form would indicate a considerable time element for development. The genera *Anaptomorphus* and *Pelycodus* appear in America as a part of the wave of migration which introduces for the first time representatives of the modern groups of mammals. Somewhat later the primates appear in England and France, apparently part of the same original stock but differing slightly as a result of independent development.

The original group of primates or ancestral stock seems to have been a large-brained arboreal insectivor, somewhat similar to the tree shrews (Tupaiidæ). Apparently their home was to the north in the Hudson Bay

[1] The considerable group termed Proglires by Osborn and including *Mixodectes*, *Microsyops*, *Cynodontomys*, *Indrodon*, *Olbodotes*, etc., all having in common the gnawing adaptation and a very primate-like set of premolars and molars, are now assigned by Matthew and Osborn to the Insectivora.

region or further north in the forest areas; and under the decidedly tropical climate which is evidenced by the palms and ferns, crocodiles and primates themselves.[2] From this ancestral center the first primates, along with other groups, migrated in all directions possible, climate and land bridges being considered. This opened three paths, one south into America, a second southeasterly into England and France, and a third southwesterly into Asia, thence ever southerly across China and India and along the Indo-Madagascar isthmus (or chain of islands) to Madagascar and Africa.

FIG. 1. Diagram of the radiation of the primates in the Eocene.

The first primates, as indicated, separate into two groups, first a group of long-headed (dolicocephalic) general feeders with unspecialized teeth, which probably took fruit, leaves, insects and small animals: and second a group of short headed (brachycephalic) fruit-eaters with crowded and rather high pointed teeth. These are

[2] For a discussion of the climate see Wortman, *Amer. Jour. Sci.*, 1903, Vol. 165, p. 417; and Wieland, same journal, Vol. 166, p. 401, 1903.

the first adaptations of the primates and it probably took some time to arrive at the degree of difference found in the Wasatch of North America.

The fruit-eating brachycephalic group includes *Anaptomorphus* of American Eocene, *Necrolemur* and *Microchœrus* of the European Eocene, and *Tarsius*, now living in southeast Asia. During the Eocene the climate was progressively colder, becoming at least temperate by the

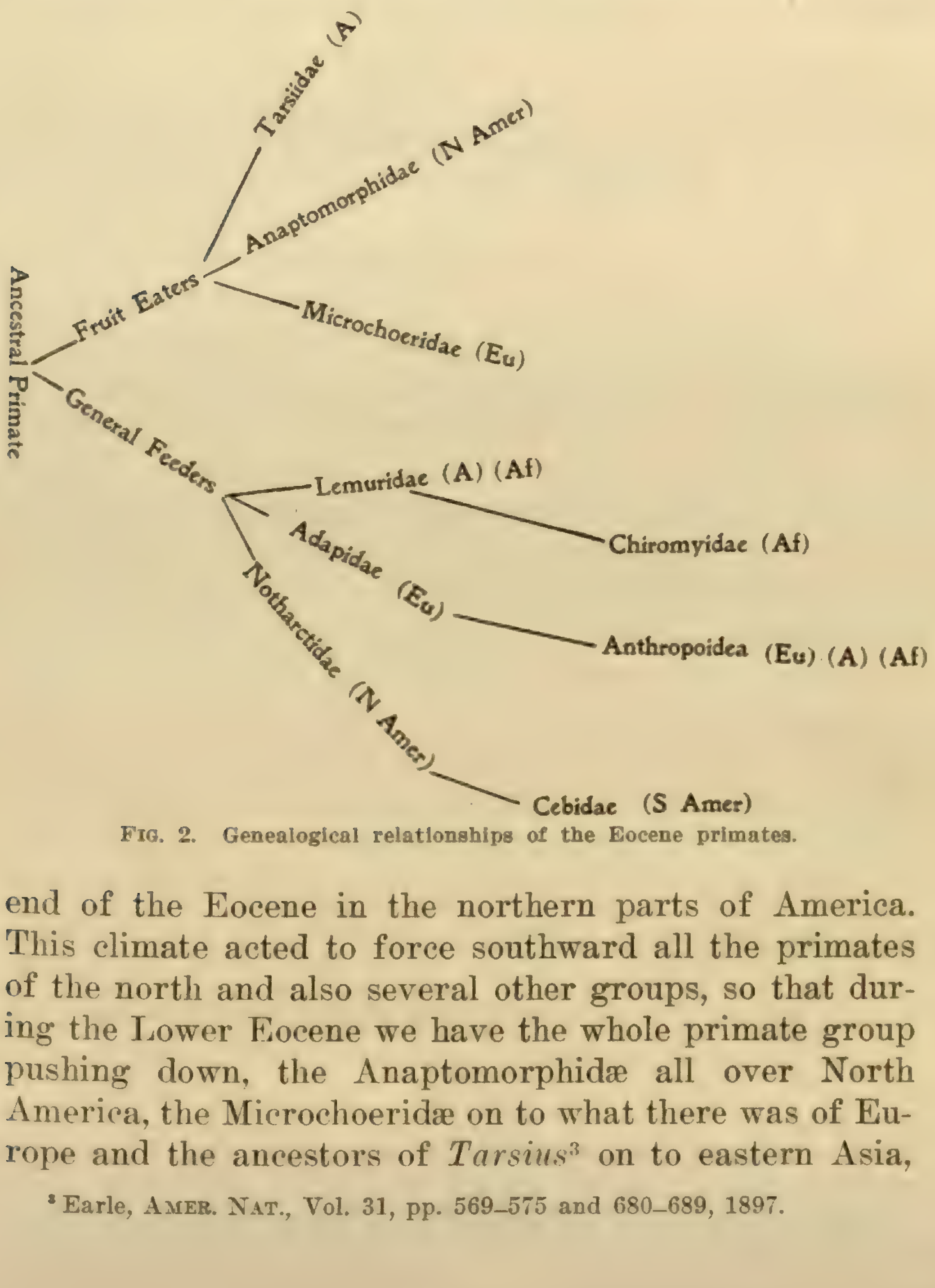

FIG. 2. Genealogical relationships of the Eocene primates.

end of the Eocene in the northern parts of America. This climate acted to force southward all the primates of the north and also several other groups, so that during the Lower Eocene we have the whole primate group pushing down, the Anaptomorphidæ all over North America, the Microchoeridæ on to what there was of Europe and the ancestors of *Tarsius*[3] on to eastern Asia,

[3] Earle, AMER. NAT., Vol. 31, pp. 569–575 and 680–689, 1897.

which through the lower and middle Eocene was separated from Europe. The fact that *Tarsius* is confined to islands possibly explains why it has remained in so primitive a condition in many ways, though specialized in the limbs which are as yet unknown in any others of this group.

The general feeders are a larger and more abundantly preserved group. It includes the Notharctidæ[4] of North America (to which belong *Pelycodus* and *Notharctus*); the Adapiidæ of Europe[5] (including *Adapis* and *Plesadapis*); the Homunculidæ[6] of South American Miocene (including the genera *Homunculus, Pitheculites, Homunculites*) and lastly the living lemurs of southern Asia, Madagascar and Africa. All have the dentition $\frac{2}{2}, \frac{1}{1}, \frac{4}{4}, \frac{3}{3} = 40$, and long heads, and apparently ate both vegetable and animal food. The group originated like the foregoing in northern America and migrated southward, driven by the change in climate. The earliest known forms are those in the Wasatch of western America, and they are likewise the most primitive. Though preserved only in Wyoming and New Mexico, they probably occupied pretty much all of our western plains country, then forested. South America seems to have been isolated from early Eocene times, so that some representatives of this group probably got into that continent by early Eocene times, *i. e.*, the radiation over North America must have been pretty rapid and general by lower Eocene times. Those in North America after the separation of South America flourished for some time, being especially abundant in the Wind River and Bridger epochs, but with the cold of the Uinta epoch they were crowded south and finally exterminated in North America, never more to be widely distributed on that continent.

[4] See Osborn, *Bull. Amer. Museum Nat. Hist.*, Vol. 16, pp. 169–214, 1902, except Hyopsodontidæ; and Loomis, *Amer. Jour. Sci.*, Vol. 171, pp. 277–285, 1906.

[5] See Schlosser, "Die Affen, Lemuren, Chiropteren, etc.," des Europäischen Tertiärs, Theil 1, s. 19–54, 1887.

[6] See Ameghino, *Anal. d. Museo Nac. d. Buenos Aires*, Vol. 15, pp. 424–429, 1906.

Those in South America quickly differentiated by the loss of the first premolar, making a dental formula of $\frac{2}{2}, \frac{1}{1}, \frac{3}{3}, \frac{3}{3} = 36$. With this also goes a deepening of the ramus of the lower jaw, a shortening of the face, and a tendency to develop the occipital region so that it overhangs widely the foramen magnum. This group of forms is termed the Cebidæ. On becoming successfully adapted to the South American continent and during the long isolation of that area, these early forms have gradually adapted themselves in various directions, often paralleling old world types. In size they have developed, the largest forms having a body of 27 to 28 inches in length, and legs as long, making a height of 4½ feet, which is a good-sized monkey. They have always remained arboreal with opposable thumbs and a prehensile tail; but they vary from the slender spider monkeys to the robust and powerful woolly monkeys (*Lagothrix*). From the above has been specialized the family of marmosets (Hapalidæ), by the loss of the last molar (making the dentition $\frac{2}{2}, \frac{1}{1}, \frac{3}{3}, \frac{2}{2} = 32$), by the development of a broad nasal septum, the loss of the prehensile character of the tail and opposability of the thumb.

The southwesterly wave of migration crossed the Behrings connection and moved down the easterly part of Asia across the Indo-Madagascar isthmus and into Africa. This isthmus or series of islands sank at or toward the end of the Eocene, leaving lemurs stranded all along the area occupied by the isthmus. Those on the islands and especially on Madagascar have remained very much as they were, adapting themselves in minor ways, but being always arboreal. Some peculiarities must have developed very early for they are common to the group, like the having of the lower incisors projecting forward (proclivous), the lower canine small and like an incisor, while the first premolar acts as a canine tooth. Then the fourth digit of the hand is longest, and the second one of the foot is clawed instead of having a nail. In this lemur group we know only the immediate

ancestors of the living forms, and as yet no record has been found of the forms intermediate between those on America and the living types. In the case of the Madagascar form, *Chiromys* or the aye-aye, we have a representative of the group which has adopted a gnawing habit to get grubs, etc., under the bark, and a great change has resulted in the dentition, by which the first incisor has become specialized into a rodent-like gnawing tooth and there is a reduction in the teeth so that the formula is only $\frac{1}{1}$, $\frac{0}{0}$, $\frac{1}{0}$, $\frac{3}{3} = 18$.

The easterly wave of migration is represented by several species of *Adapis* found in the middle and upper Eocene of England and France. Apparently the progress of this easterly migration was slower, so that they reach Europe considerably later than the same latitude in America. The primates are not in the front wave of immigration on the European side, so that it is possible that the forested condition was not as favorable. The Adapiidæ in Europe, small primates with a long low skull and the ancestral dental formula $\frac{2}{2}$, $\frac{1}{1}$, $\frac{4}{4}$, $\frac{3}{3} = 40$, the teeth being very generalized.

With the close of the Eocene the first adaptive radiation of the Primates was complete, and they had achieved an almost world-wide distribution. At the end of the period the North American contingent was extinct, the South American group was isolated, the Asiatic and African forms were scattered on islands and on the African continent, and the European contingent was located in central and southern Europe, or what land there was at that time in those regions (see Fig. 3); and it is among these that the next act in the great primate drama took place.

The Oligocene period is one in which there was a gradual rising or emergence of continental areas so that the southern part of Europe was an archipelago, which toward the end developed into a long peninsula, extending from the present Asia Minor (see Fig. 3). During this period the change in the Adapiidæ is but little known, but

during that time they shortened the skull and lost the first two premolars, and made a considerable increase in size. In Europe their remains are very scarce and confined to the Lower Oligocene when it was the true *Adapis* which was holding over from the Eocene. Schlosser has just reported some primates from the Fayûm formations of Oligocene age in northern Africa. These he gives new generic names, *Mœripithecus, Parapithecus* and *Proplio-pithecus,* assigning the first two to the Cercopithecidæ and the last to the Simiidæ. They seem from the descriptions to be primitive members of the Cercopithecidæ, which would indicate that the change to the modern type by the loss of the first two premolars was accomplished in the early Oligocene, perhaps in Africa as the two areas are in connection at the time across Gibraltar.[7]

At the beginning of the Miocene the European primates had the dental formula $\frac{2}{2}, \frac{1}{1}, \frac{2}{2}, \frac{3}{3} = 32$, a shortened face, and a shortened tail, but were still arboreal forms. During the Lower Miocene two divisions arise, the one adhering to the quadrupedal gait, the heavy jaws and longer snout: the other acquiring the bipedal gait, and shortening the face with a corresponding broadening of the teeth. In both divisions there is a tendency to come down to the ground.

The former group is the Cercopithecidæ in its broad sense, or "old world monkeys"; while the latter are the Simiidæ or apes.

The Cercopithecidæ seem to run back to some such form as the *Oreopithecus,* found in northern Italy, and presenting dental characteristics resembling the baboon, but at the same time having a shortened face suggesting the Simiidæ. A second form belonging to this group is *Mesopithecus* found in considerable abundance in the Lower Pliocene of Greece. This form seems to be intermediate between the macaques and langurs, resem-

[7] For geography see Matthew, *Bull. Amer. Museum Nat. Hist.,* Vol. 22, p. 364, 1906. For the Fayum Primates, see *Zoologischen Anzeiger,* Bd. 35, for March, 1910, and Matthew, AMER. NAT., Vol. 44, Nov., 1910, p. 700.

bling the former in the stout limbs, the latter in its dentition. Considering the different subfamilies it would appear that the Cercopithecidæ originated in southern Europe, that it was fairly successful, and that as a result of this, the family adapted itself in three directions; first one group left the trees and took to life on the ground, giving rise to *Cynocephalus* and *Macacus;* the second group became leaf feeders, and developed a pouched stomach and for some reason also disproportionally long hind limbs, giving rise to *Semnopithecus* and *Nasalis* of Asia and *Colobus* of Africa: while those remaining in the trees and changing but little are *Cercopithecus* and *Cercocebus* of Africa.

The differentiations took place in the Miocene and are fundamentally based on food supplies. Those forms which had developed strength enough to defend themselves, their fore and hind limbs being approximately equal in length, and their food including insects, lizards, frogs, etc., as well as all sorts of vegetable life, like leaves, fruit, blossoms, etc., came down from the trees.

The terrestrial forms which continued to live in the forests make the genus *Macacus,* or macaques, which during the Pliocene spread pretty well all over Europe, even up into England, and also into western Asia where they still live. In the Pleistocene some representatives of the genus went with the great wave of migration from southern Asia into Africa, but they have become extinct in that continent except for one species, the Barbary ape. Those members of the group which left the woods and took to the more open country developed great strength and powerful jaws and are the baboons (*Cynocephalus*) These too originated in southern Europe and migrated during the Pliocene eastward into Asia, and during the Pleistocene on down into Africa, to which continent they are now confined.

The second subfamily of the Cercopithecidæ are the langurs (*Semnopithecus, Nasalis* and *Colobus*) which, while remaining largely arboreal, have specialized as her-

FIG. 3. Diagram of the radiation of the quadrupedal old world monkeys.

bivors among the primates, feeding exclusively on leaves; in response to which they have developed a stomach of several pouches comparable to that of a sheep or cow. Like the preceding subfamily, they originated in southern Europe and during the Pliocene moved over into southern Asia, where the langurs and the nasal monkeys live to-day. Some members of the group, however, moved during the Pleistocene in Africa where the thumb was much reduced, which feature distinguishes the genus *Colobus*.

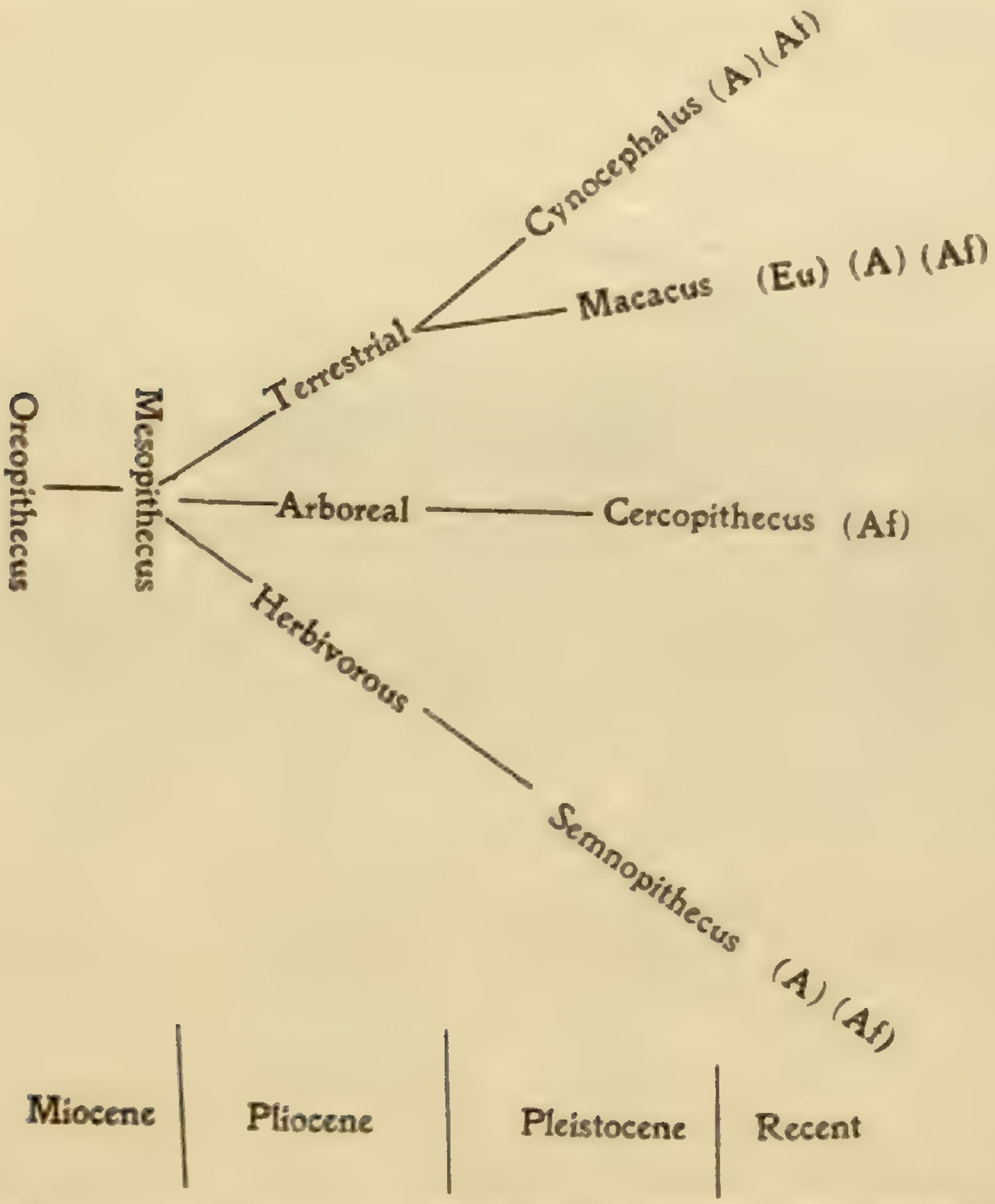

FIG. 4. Genealogical relationships of the quadrupedal old world monkeys.

Lastly the unspecialized subdivision of the family, the *Cercopithecus* genus, followed the same lines of migration and reached Africa where they now live, having spread over the major part of the continent.

Turning back to the early Miocene, we find that there

was another group of primates which tended to come to the ground, and these tended to assume a more or less upright position, with a bipedal gait. The hands thus free to take hold of objects, were free to develop a deftness and adaptability, which seems to be the key to the progressive development of the apes. It seems however that this handling of objects (food, sticks, stones) began before they left the trees and was really the cause of taking the bipedal gait. The climbing offered an ever changing grasp and carrying food to the mouth was a natural starting point; so that, with the front paws used as hands, there is a good reason for exempting them from the heavy work of locomotion. Contributory to this idea is the eolith development. These crude flaked flints[8] begin back in the Miocene at least, and as Penck[9] suggests the only known primate which might be suggested as an eolith-maker is *Dryopithecus*. It seems highly probable then that the hands had begun to be used as such before the first apes came to the ground and that this specialization of the hand was the cause of the upright position and bipedal gait. Of course the varied experience resulting from taking up all sorts of objects and using them for different purposes tended to develop the intelligence, and that furthered handling, the two acting and reacting on each other.

In the early Pliocene of southern Europe three divisions of the simian group have already arisen,[10] one group remaining arboreal, or more probably reverting again to the trees, a second group developing great muscular and skeletal strength, the third group developing especially the brain and central nervous system.

The first of these groups, *i. e.*, the retrogressive or aboreal group, is represented in the Upper Miocene of southern Europe by *Pliopithecus*, a form ancestral to the modern gibbons, and one which during the upper Miocene

[8] See MacCurdy, *Amer. Anthrop.*, Vol. 7, n. s., pp. 425–479, 1905.

[9] *Science*, Vol. 29, n. s., p. 359, 1909.

[10] See Schlosser, *Zoologischen Anzeiger*, Vol. 22, p. 289, 1900.

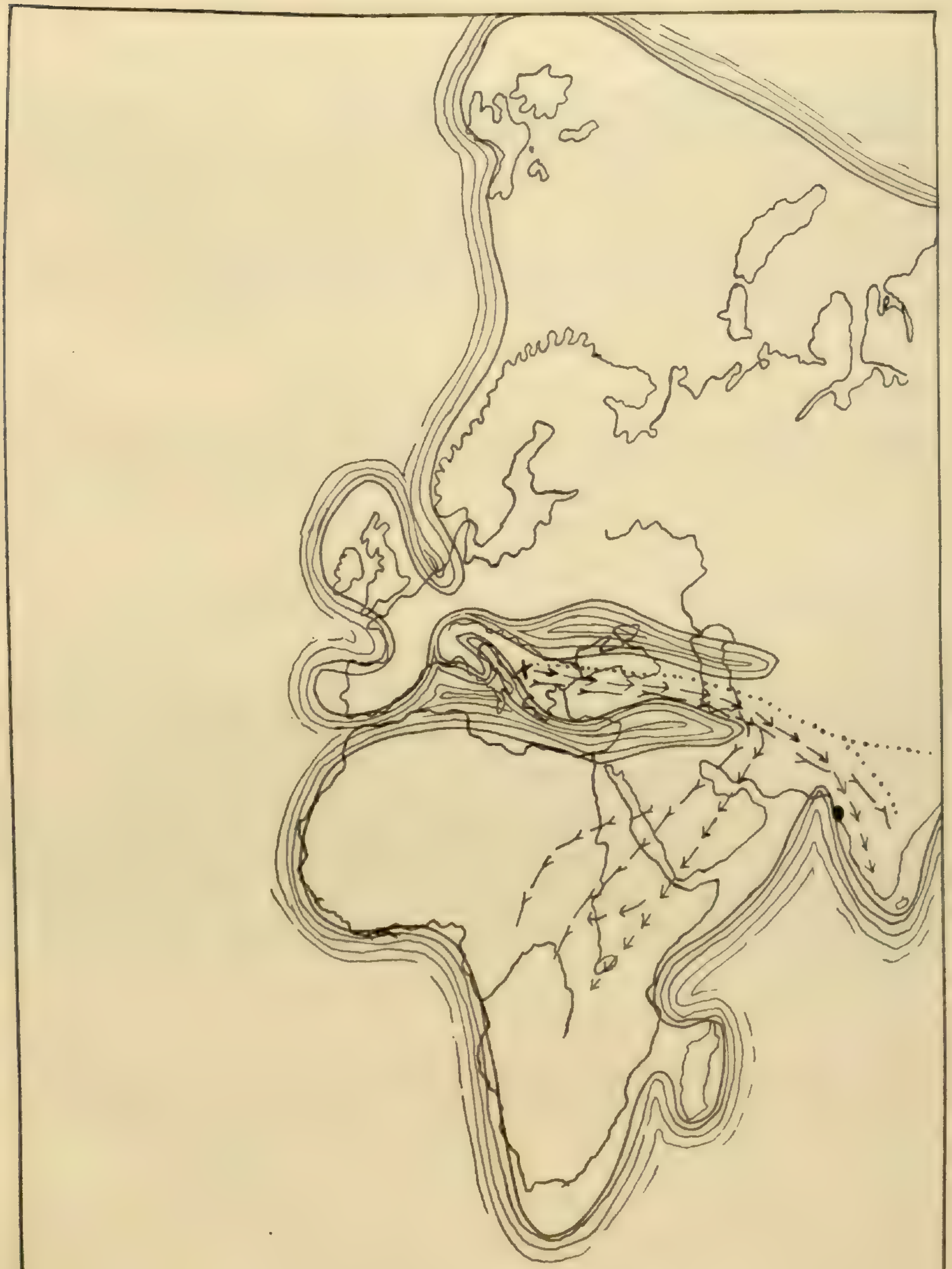

FIG. 5. Diagram of the radiations of the bipedal primates or apes.

and lower Pliocene spread over a large part of Europe (France, Germany, Switzerland). However when the colder climate of the Pliocene developed, the European contingent was exterminated, and only those in Asia have survived as the gibbons of to-day.

The second group which developed especially strength is rare both in prehistoric and recent times: but it seems

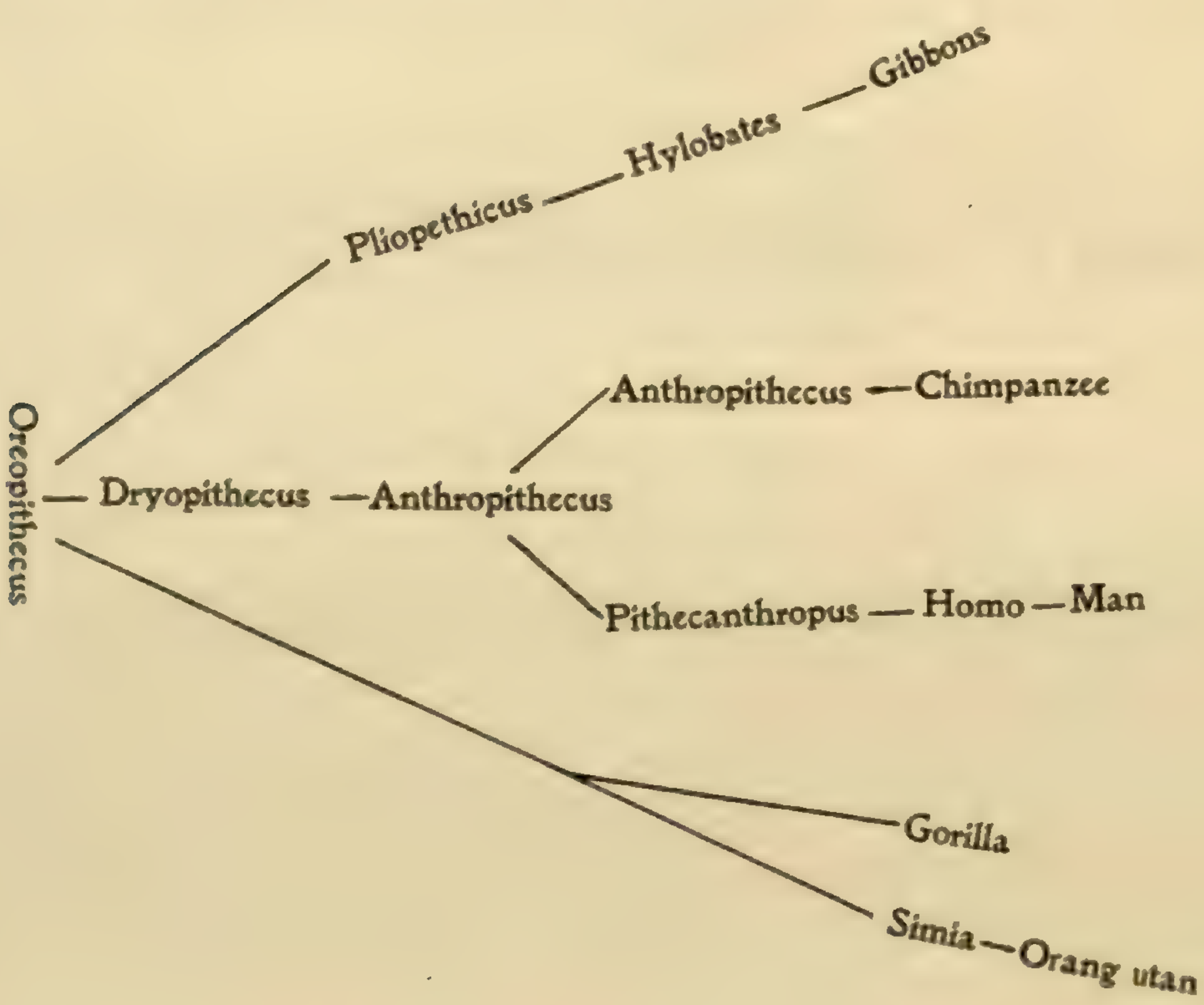

FIG. 6. Genealogical relationships of the anthropoid apes.

to have originated first in southern Europe though no representatives have yet been found. In the Pliocene however the genus *Simia* has been found in southern Asia where its representatives still remain as the orang utan. During the Pleistocene representatives of the group seem to have reached Africa where they have persisted as the gorilla.

The third group has at its base *Dryopithecus*, the middle and upper Miocene ape which ranged over a con-

siderable part of Europe: but at the end of the Miocene this form became extinct and with it the last of the chimpanzee line in Europe, the next representative being *Anthropithecus*, the true chimpanzees, found in the Pliocene of India. This first chimpanzee makes a slightly closer approximation to man than the living species. During the Pleistocene the wave of immigration into Africa included *Anthropithecus*, which has survived only on that continent. In 1896 Dubois found in Java in beds now generally called early Pleistocene, the top of a skull, a femur, and a few fragments of a transitional form which is in many ways like the apes and in others like man. This he called *Pithecanthropus erectus*, and it stands as either a very high grade ape or as a low grade man, the latter being the usual designation. If not the actual ancestor of man, it is at least a typical stage in his development.

From the distribution of *Anthropithecus* and *Pithecanthropus* it seems certain that man originated in southern Asia, at least by the beginning of the Pleistocene: and that he radiated from there westward across Europe where such remains as the Heidelberg jaw, and those of the Neanderthal type have been found so widely. He probably also migrated easterly into North America, and thence south with the Pleistocene fauna into South America where very primitive remains have recently been described by Ameghino as *Diprothomo platensis*, and *Homo pampensis*. Remains have been strangely scarce in North America, though the fauna, with which early man usually associated is present in various parts of the continent.

JEAN MARCHANT; AN EIGHTEENTH CENTURY MUTATIONIST[1]

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JEAN MARCHANT was the son of Nicholas Marchant (died, Paris, 1678), director of the Jardin du Roi, the principal author of the famous "Mémoires pour servir a l'histoire des Plantes," published in 1676 under the auspices of l'Académie royale des Sciences and edited by Dodart.[2]

The name Marchant is perhaps most familiar in connection with the genus *Marchantia,* which, though not unfrequently attributed to Linnæus, was named by Jean Marchant in honor of his father,[3] when, because of his discovery of the "flower" and "seeds," he removed it from the genus *Lichen,* under which it formerly had figured as *Lichen petræus stellatus.*[4]

[1] Contribution from the Botanical Laboratory of the University of Michigan, No. 121.

[2] Clos, D., "Les trois premiers botanistes de l'Académie royale des Sciences, Dodart et les deux Marchant," *Bull. Soc. bot. France,* 35: 285, 1888. In this paper Clos goes to great length in a successful attempt to show that Nicholas Marchant was the chief contributor to the work just referred to, though a simple reference to a statement on the part of the academy and which curiously enough seems to have escaped him, would at once have settled the matter beyond question. In "Table Alphabétique des matières contenues dans l'Histoire et les Mémoires de l'Académie Royale des Sciences," publiée par son ordre, 1: 200, 1666–1698, 1778, one reads: "Marchant [M. Nicholas] a fourni tout le Botanique des Mémoires pour servir à l'Histoire des Plantes. T. 4, p. 122."

[3] Marchant, J., "Nouvelle découverte des fleurs et des graines d'une plante rangée par les botanistes sous le genre du Lichen," *Mém. de l'Acad. roy. d. Sc.,* 1713, pp. 229–234. "Nous établirons pour cette plante un nouveau *genre* que nous appellerons *Marchantia* du nom de feu M. Marchant, mon père, qui le premier eut l'honneur d'occuper une place de botaniste dans cette Académie, lorsque le Roy en 1666 créa cette Compagnie."

[4] Caspar Bauhin, Pin. 362.

It was indeed a discovery far beyond mediocrity and indicative of excellent powers of observation. For since the days of Cæsalpino but little advance seemed to have been made as to the organs of reproduction. Even one of Linnæus's first papers, "Præludia Sponsaliorum arborum," deals with the sexes of plants, and, attracting the attention of Olaf Rudbeck (1729), secured for the "father of botany" *in spe*, the position of assistant.[5]

Darwin, in the introduction to his "Origin of Species," points to Buffon as the first transmutationist, though, as he says, it was the views of Lamarck which first attracted general attention. But long before their time, when Buffon was but a boy of twelve, Jean Marchant had made some very pertinent observations on the sudden origin of species. Believing genera to have been created as such, a view expressed in his early days by Linnæus himself in his "Systema Naturæ,"[6] he was able to see new "species" originate suddenly. He had at his disposal a garden, probably already used by his father,[7] who was an ardent collector and introduced the seed of many foreign plants, growing and describing them.[8] His observations were made upon *Mercurialis annua*, the dog's mercury,[9] a plant long known as possessing certain reputed virtues.[10]

[5] Wittrock, Veit B., "Nagra ord om Linné och hans betydelse för den botaniska Vetenskapen," *Acta Horti Bergiani*, 4: No. 1, 1907.

[6] Genus omne est naturale, in primordio tale creatum."

[7] Presumably the "Jardin du Roi." "Il [Nicholas Marchant] faisoit cultiver au Jardin Royal celles qui ne se trouvoient que difficilement à la campagne," *Hist. de l'Acad. roy. d. Sc.*, 1666–1686, 1: 200, Paris, 1733.

[8] "Hist. de l'Acad. roy. d. Sc.," 1680, p. 307.

[9] This term is also used for *M. perennis*, in which case the name French mercury is given to *M. annua*.

[10] It was supposed that the juice of species of *Mercurialis*, especially of the Mediterranean *M. tomentosa*, had the power to determine the sex of children, according to whether the mother drank the juice of the male or of the female plant. Unfortunately the true sex of the plant was not known, as also is apparent from Marchant's paper. Thus boy's mercury was the name applied to the female plant of *M. annua*, girl's mercury the name given to the plant with staminate flowers. Also, staminate flowers repeatedly have been observed on the pistillate plant (*f. ambigua*, Duby, "Bot. Gall.," 1: 417).

In 1715 Marchant noted in his garden[11] the appearance of a laciniate form of *Mercurialis annua,* which he designated *Mercurialis foliis capillaceis.* The next year, in the same part of the garden, this plant reappeared, being represented by four individuals. There appeared further two plants, the foliage of which, though also of a laciniate character, was sufficiently different to permit of their being readily distinguished. To these plants he applied the name *Mercurialis foliis in varias et inæquales lacinias quasi dilaceratis.* The description of the leaves at once leads us to recognize this plant as a typical laciniate form, especially his reference to "a large number of leaves, which, because of their irregular outline, resemble mere remnants of leaves torn or gnawed by caterpillars," curiously enough, the same expression which I used to describe the appearance of the leaves in the flowering shoot of *Arctium minus laciniatum.*

In an attempt to explain the successive appearance of these two new forms of *Mercurialis* we could assume that both forms had been created in 1714, but that the seed of one had germinated in 1715, while that of the other remained dormant for a year. It is, however, far more probable that but one plant of the first laciniate variety had been allowed to grow up, and that in the next year special orders were given to the gardener who had the care of this particular portion of the garden, to allow to grow all seedlings which in the least resembled those of *Mercurialis.* Still another possibility is that the first form, created in 1714, gave rise, in 1715, through a second mutation, to another, less laciniate form, which appeared in 1716.

After reporting these plants in 1719, Marchant makes no further mention of them, but de Candolle[12] refers to them, under *Mercurialis annua,* in the following terms:

[11] Presumably the Jardin Royal. "Jean Marchant avait, ainsi que son père, le titre de directeur de la culture des plantes du Jardin du roi." Michaud, "Biog. Univ.," 26: 486, 2d ed.

[12] "Prod.," 15: 797.

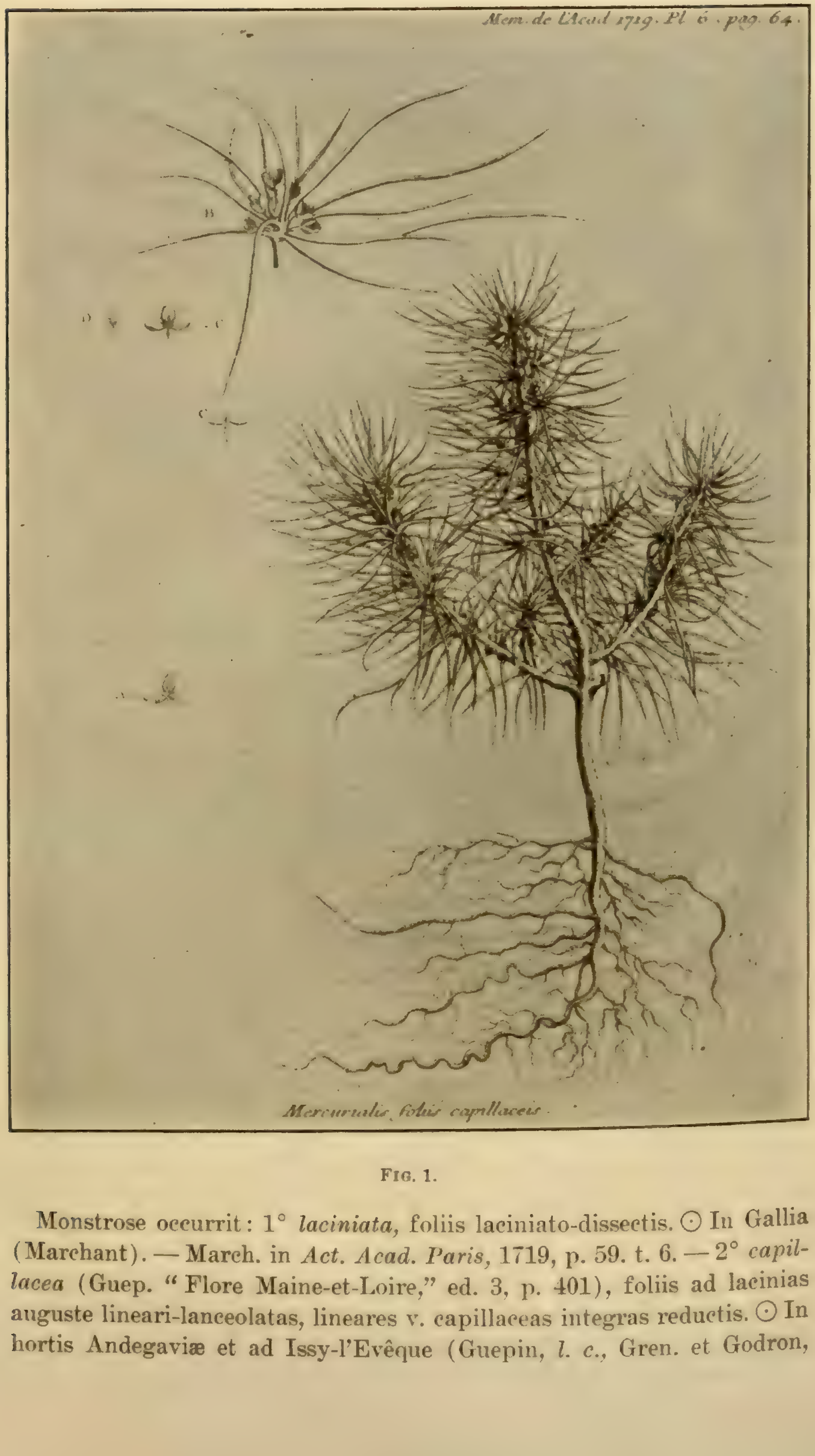

FIG. 1.

Monstrose occurrit: 1° *laciniata,* foliis laciniato-dissectis. ☉ In Gallia (Marchant). — March. in *Act. Acad. Paris,* 1719, p. 59. t. 6. — 2° *capillacea* (Guep. "Flore Maine-et-Loire," ed. 3, p. 401), foliis ad lacinias auguste lineari-lanceolatas, lineares v. capillaceas integras reductis. ☉ In hortis Andegaviæ et ad Issy-l'Evêque (Guepin, *l. c.,* Gren. et Godron,

FIG. 2.

"Flore de France," Vol. 3, p. 99). — Marchant in *Mém. de l'Acad. Paris*, 1719, p. 64, t. 6.

This discovery on the part of Marchant is particularly interesting for various reasons. In the first place be-

cause it is the second historical case of mutation on record. Further, because of a certain analogy with Sprenger's discovery of *Chelidonium majus laciniatum*.[13] Sprenger, an apothecary of Heidelberg, cultivated a large number of plants in his garden as was the custom in those days, and, about 1590, observed there a type of *Chelidonium majus* formerly unknown to him and to which he gave the name *Chelidonia major foliis et floribus incisis*. Tournefort, in his "Schola botanica," mentions three forms, *Chelidonium majus vulgare* C. B., *Ch. majus foliis quernis* C. B. (*Ch. folio laciniato* J. B.) and *Ch. majus foliis et flores minutissime laciniatis* Hort. reg. par. The second of these was identical with the variety discovered by Sprenger, the third a form which had originated in the Paris Botanic Garden and was distinguished from the other by the greater reduction of the leaf blade. Of the laciniate varieties of both *Chelidonium majus* and *Mercurialis annua* there exist therefore two forms. While those of *Chelidonium majus*, and especially the first, are fairly well known and may be encountered in almost any botanic garden, it is not so in the case of either of the laciniate varieties of *Mercurialis annua*. At least I do not remember seeing them, nor do I recollect the occurrence of their names in the seed-exchange lists annually published.

In at least one instance the claim has been made that one of the laciniate varieties of *Chelidonium majus* originated *de novo*[14] a claim which to Korschinsky[15] appears to lack foundation. No such claim has been made for one of the laciniate varieties of *Mercurialis annua*. However, as seen from de Candolle's account, given above, at least one of the laciniate forms was reported as occurring both in the botanic garden at Angers and also at Issy-l'Evêque. These two towns, the first in Maine-et-Loire,

[13] Roze, E., "Le *Chelidonium laciniatum* Miller," *Journ. de Bot.*, 9: 296, 1895.

[14] Clos, D., "Réapparition de la Chélidoine à feuille de Fumeterre," *Compt. rend.*, 115: 381, Paris, 1892.

[15] Korschinsky, S., "Heterogenesis und Evolution," *Flora*, 89: 240, 1901.

the other in Saône-et-Loire, lie more than 200 miles apart. It is possible, perhaps, that the seed was brought from Paris to Issy-l'Evêque and from there transported accidentally to Angers. Or is it more probable that the variety originated a second time? It is a question which forever must remain unanswered, though it is not improbable that a French student, who most readily commands the means of research in this direction, could, by delving into historical records, perhaps throw some light upon the subject.

The work of Jean Marchant gives evidence, not only of great exactitude, but also of excellent powers of observation. Thus, a few years after his discovery of the laciniate forms of *Mercurialis annua,* he was able to give an account, and, as I believe, the first, of a myxomycete, of the "flowers of tan."[16]

As is evident from the description and drawings, he was dealing with a *Fuligo.* He recognized the vegetable character of the organism, but unfortunately places it with the sponges, giving it the name *Spongia fugax, mollis, flora et amoena, in pulveri coriari nasceus.* In this case, as in the other, Marchant's ambition did not lead him beyond a mere, apparently most accurate, description, something decidedly pleasing when we remember that in the same year Jean Marchant was elected to membership of the Académie (1678), there appeared Father Kircher's *Mundus subterraneus,*[17] and that one of his contemporaries was de Maillet (1656–1738), who "derived birds from flying fishes, lions from sea-lions, and man from *l'homme marin,* the husband of the mermaid!"

Believing genera to have been created as such, Marchant did not go beyond this point, but realized that species were derived from preexisting ones. His own

[16] Marchant, J., "Observation touchant une végétation particulière qui nait sur l'écorce du chêne battue, et mise en poudre, vulgairement appelée du Tan," *Mém. de Math. et de Phys. de l'Acad. roy. d. Sc.,* 1727: 335, Paris, 1729.

[17] Osborn, H. F., "From the Greeks to Darwin," 109, 1908. "The worthy priest describes orchids giving birth to birds, etc."

words should be quoted here. As far as I am aware, there exists but one account of any length of Marchant's discovery, that of Korschinsky.[18] Godron refers to him[19] as does de Vries.[20]

Since the original papers are rather inaccessible to the majority, it was deemed of interest to give here a translation of Marchant's two articles dealing with his discovery. The translation of course has been made as literal as possible. The first paper is merely a résumé of an address made before the academy by Marchant. The second gives a detailed account as published in the *Mémoirs*.

ON THE PRODUCTION OF NEW SPECIES OF PLANTS[21]

In the month of July, 1715, Mons. Marchant noted in his garden a plant which he did not know, and which attained a height of from five to six inches.[22] It persisted until the end of December, when it dried up and died. He believed to be able to class it only with the genus to which the mercury belonged; and since it was entirely new and thus far had not been described by authors, he called it *Mercurialis foliis capillaceis*.

The following year in the month of April, and in the same place where this plant had been, he saw appear six others, of which four were quite similar to the former, and two others sufficiently different to make another species of mercury, which he named *Mercurialis foliis in varias & inæquales lacinias quasi dilaceratis*. It persisted until the end of December, in which respect these two species are different from the common mercury, which, though annual like these, does not last as long.

[18] *Loc. cit.*

[19] Godron, "De l'espèce," 1: 160 (not seen).

[20] De Vries, H., "Die Mutationstheorie," 1: 136, 1901. "*Mercurialis annua laciniata* ist 1719 von Marchant als neue Form entdeckt worden; sie ist seitdem samenbestandig geblieben."

[21] "Hist. de l'Acad. roy. d. Sc.," 1719, p. 57, Paris, 1721.

[22] The French "pied" is equal to 1 foot 1⅛ inch of our measure and is divided into 12 "pouces," each "pouce" being divided into 12 "lignes." Pouce and ligne are translated inch and line, respectively.

These two new plants since have multiplied in a space of seven or eight feet, and, which is astonishing, never has Mons. Marchant been able to discover any signs of seed upon them. At the same time the slight extent of the plot upon which they reappear every year sufficiently shows that they must have been derived from seeds which probably fell upon it from preceding plants. Since some time ago were discovered the secret means which several plans make use of to hide their seed, it is all the more marvelous that there still are some which can succeed in hiding them.

But the principal reflexion of Mons. Marchant upon these two plants is that it would not be impossible for new species to be formed; for these have all the appearance of being such; how else could they have escaped all botanists? Art, culture and, still more, chance, that is to say, certain unknown circumstances, every day bring about novelties in interesting flowers such as the anemones and buttercups, and these novelties are treated by botanists as varieties only, which do not deserve to change the species; but why should nature be incapable of novelties which went thus far? It seems she is less constant and more diverse in plants than in animals, and who knows the limits of this diversity?

At this rate the old-time botanists would not have been wrong in describing so few species in a single genus; they were not acquainted with more, and it is time which has brought new ones. For the same reason the future botanists would be overwhelmed, and finally obliged to abandon the species to limit themselves to the genera. But ere forecasting that which will be, one must assure oneself of that which is.

Observations on the Nature of Plants

By Mons. Marchant[23]

The researches which are made in Natural Science frequently demand long series of observations to arrive at a perfect knowledge of the sub-

[23] "Mém. d. Math. et de Phys. tir. d. Rég. de l'Acad. roy. d. Sc. de l'Année, MDCCXIX," p. 59, Fy. 1, 1719, Paris, 1721.

jects which one undertakes to deal with; and it is for this reason that one must not be astonished that the botanists have not yet discovered the seeds of a number of plants, though they knew these plants long since. One must be the less surprised about this since among these plants, there are several which can not be cultivated, and with which one meets accidentally only, and others which, because of their smallness, also bear only exceedingly small seeds, which frequently escape even the most observant. The observation of which we are about to speak is related to these kinds of investigations. It is in fact a matter of two plants which we deem to be of the same genus, but of different species, of which during the four years which we have known them, which we have studied them, it has been impossible for us to observe the seeds. These plants showed themselves to us for the first time in our garden; I had never seen them before, neither there nor in other places, and I do not know that botanists have made mention of them.

Yet they are sufficiently tall to be observed by those who apply themselves to a knowledge of the Simples, if they grew commonly in our gardens, just as are a number of other common plants; these new plants finally have reproduced themselves in our garden, from the time above mentioned, without one having been able to find seed upon them.

According to the smell of these plants and the structure of their flowers, I am satisfied they belong to the genus of the Mercury of which we here represent the flower (Fig. A, Pl. 1). To make known the nature of these herbs, we will begin by describing the first species which we observed in the month of July of the year 1715, and we shall name it *Mercurialis foliis capillaceis.*

The plant was five to six inches high, its stem was about two lines in thickness, bare at the base, round, of a pale green color, smooth, shiny and nearly transparent, provided with five branches, two of which, parallel and placed towards the base of the stem, were longer than two inches. The others were unequally shorter. The stem and the branches were rather irregularly beset with leaves without petioles, some alone and bare (*les unes seules et nues*), the others attached in bunches and intermixed, accompanied at their point of origin by several flower buds, which together, or leaving some spaces between them, surrounded the stem and the branches of this plant. The longest leaves ending in a sharp point measured about one inch, their width was half a line in the middle, some were wider at their base; some others were dissected towards the point in two very narrow strips of different lengths, and all of them were of a green-brown color, smooth, shiny and slightly indented along their length. These leaves pointed in this or that direction without order, some with the tip turned upward, the others downward, and others bent in sickle-like form. The smallest were placed horizontally. All were rather stiff, notwithstanding their delicate texture, and they appeared more or less like the principal veins of leaves

which had been stripped of their lateral veins and of their parenchyma. The flowers which were collected in small clusters (*B.* nat. size) opened successively only. Their color approached a greenish yellow. They consisted of a calyx of three leaves *C* of an oval shape, shell-like, separated from each other at their point of origin by a cluster of ten or twelve very fine and very short filaments *D* which had no tips.[24] The flower was but a line in diameter and its pedicel was so short that it was hardly visible.

The root of this plant was a little less thick than its stem. It was from four to five inches long, twisted, forming slight undulations throughout its whole length, accompanied by several fibers similarly undulating and hairy, which branched of in all directions. Its internal substance was very white, hard and covered with a more or less fleshy bark of a white-yellow color.

The entire plant on being rubbed had a rank unpleasant odor and a nauseous flavor having something nitrous about it, closely approaching the taste of the common Mercury.

This plant persisted until the end of the month of December, after which it dried up and perished entirely.

This observation put me on the alert to discover this plant the following year. Until the end of the month of March I noticed nothing of that for which I was looking; but in April I saw appear six plants, of which four seemed to be the plant which just now has been described. The two others were slightly different from the preceding, in that they had larger leaves. These and the others increased in size, and I had the pleasure to observe among these six plants a second species which as yet was unknown to us, as will be seen from the following description; and since this time these two species of plants reappear every year without cultivation in the same portion of the garden. We shall name this second species, *Mercurialis altera foliis in varias & inæquales lacinias quasi dilaceratis.*

It produces a root three or four lines in diameter and six inches long, knotty, provided from its upper portion with several fibrous roots of the same length, much contorted in small equal undulations, which twist towards the bottom of the soil, covered by a quantity of hairy fibers, which extend laterally around the root. Their surface is composed of a chapped, fleshy pellicle of a dirty-white color, which covers a coriaceous and very white woody body, without the slightest indication of pith. From this root there arises immediately a stem about a foot high, a little less thick than the root, hard and woody, covered by a fleshy bark, shiny and smooth, of a pale green color, containing a greenish pith. This shoot from its point of origin to its extremity is furnished

[24] "*. . . qui n'avoient point de sommets*"; sommets, transl. tips, anthers, *apices* of Dodonæus.

with a number of branches, which together form a sort of very small tufted bush, about eight to ten inches in diameter. These branches are arranged upon the stem without regular order, just as the other little branches which they bear, which frequently are subdivided; and nearly all these branches are slightly thickened at their point of origin. An infinite number of clusters of leaves, arranged along the branches and their divisions and subdivisions, covers this little bush. The leaves resemble each other but little. The larger ones, placed near the base of the branches are an inch long and more, measuring one, two or three lines at their greatest width, and in the whole lot there are some which do not measure a third of the width of the preceding. They are all without petioles, and terminate in a very sharp point, having but very slight traces of veins in the middle, which nevertheless are firm and hard, in comparison with their thickness.

The larger of these leaves have as many as four or five incisions. Some are very deep, forming sharp reentering angles and rounded lobes (*formant des angles, rentrans aigus, & des saillans arrondis*). The other incisions, on the other hand, have obtuse reentering angles and very sharp lobes (*les angles rentrans obtus, & les dentelures saillantes fort aiguës*). Several others of these leaves have but one or two incisions, or even but slight crenations not very deep or undulating; and finally a large number of leaves because of their irregular outline, resemble remnants of leaves torn or gnawed by caterpillars.

From the center of each cluster of leaves appears a mass of from twelve to fifteen or twenty flowers collected together, from between which there arise some small, simple and very narrow leaves, in the manner of small strips terminating in a sharp point.

The flower *A* (natural size, Pl. 2), of which the pedicel is very short, consists of a calyx composed of three small leaves (Fig. *C*) of an oval shape, shell-like, of a green-yellow color. In their axils occur from twelve to fifteen filaments *B* of the same color, without tips and two of these filaments always diametrically opposite, being twice the length of the others. The full-blown flower is about one line in diameter. The entire plant is of a brown-green color, mixed with a yellow tinge. Its taste is insipid with a slight nitrous flavor.

These two plants are annuals; at the same time they last much longer than the common Mercury, since they have been observed to germinate in April, and remain green until the end of the month of December.

They resemble each other greatly because of their flowers, their smell and the consistency of their leaves; but they differ exceedingly by their aspect, and, as has been said, in regard to the outline of their leaves.

The opinion commonly held by botanists is that the male Mercury bears seeds and produces no flowers, and that it produces equally the male and the female Mercury, instead of which the female Mercury

bears sterile flowers only, that is to say, that it does not produce seeds.

On this principle, our two new plants on which we have seen flowers only, would be female Mercuries, resulting from seeds of the male Mercury; but under these circumstances it would be rather difficult to understand why these two plants reappear in this garden only in the same space of seven or eight feet of ground, where they were discovered the first time, since the common male and female Mercuries germinate and grow in great abundance in all the gardens; which would lead one to believe, contrary to the opinions of modern botanists, that the two plants of which we here give descriptions, bear seeds, because they reproduce themselves without aid in this spot, for certainly they are not found anywhere else.

We shall continue our observations on this phenomenon; and in the meantime, we shall propose a few conjectures on the large number of species we believe plants may give rise to.

The men of science who are interested in plant culture, and especially those who are fond of plants which bear beautiful flowers, such as the anemones, tulips, carnations and other flowers, well know that the seeds of these plants, being sown, frequently produce pleasing and interesting diversities. Nature, without regard to the beauty of the flowers, behaves in the same manner in the diversity of the species of which it increases the number in the Herbs or Simples.

The instance of our two plants indicates this sufficiently, since in four years we have witnessed the birth of two constant species which were unknown to us.

Because of this observation there would be reason to believe that the Almighty once having created individuals of plants as a model for each genus, made up of all imaginable structures and characters, capable of reproducing their like, that these models, I say, or types of each genus, in perpetuating themselves, finally had produced varieties, among which those which have remained constant and permanent, have constituted the species, which as time went on and in the same manner, have made other different productions which have so increased Botany in certain genera, that it is a fact that to-day there are recognized in some genera of plants as many as one hundred, one hundred and fifty, and even as many as more than two hundred distinct and constant species belonging to a single genus of plants.

The proof of that which is suggested on the subject of the production of species seems all the more well founded, when one remembers that the most ancient botanists have mentioned but about four hundred types of genera of plants, to which they add few species, which leads one to believe that at that time the species were as yet not very numerous; since at present we know more than eight hundred types of genera, to which must be added thirteen or fourteen thousand species or more,

among which, it is true, several are mere repetitions, and others are but simple varieties.

One may be sure that botanists, in going through countries which formerly were unknown, will discover new types of genera of plants from the point of view of the physicians, though created many centuries ago, as well as an immense number of species which will have arisen from them. Which, in time to come, and according to the conjectures made above, would tend to reduce Botany to a knowledge of the types of the genera only, giving up the species, to evade the confusion to which they might give rise in this science.

Yet whatever might result from this, we must profit by the new discoveries, to illustrate the history (evolution) of plants.

The species may have still other uses, though it is true that the majority of plants, of which use is made in medicine, are ordinarily those which are called type of the genus, because they are the first in which certain virtues and distinctive characteristics have been recognized, which constitute each genus of plants; but since because of lack of genera, species frequently are substituted for them in Pharmacy, one must not neglect a knowledge of the species, even though there are no living organisms in Nature which increase more abundantly and who make more diversities than do plants, as has been said, always if one excepts Insects, which apparently reach a greater number, but which are not so well known to us as are plants.

NOTES AND LITERATURE

NOTES ON HEREDITY

Miss Wheldale presents an interesting theory concerning the formation of anthocyanin.[1] The theory for which a good deal of evidence is presented is that of the reversible reaction

$$\text{Glucoside} + \text{water} = \text{chromogen} + \text{sugar},$$

which is controlled by one or more enzymes.

Whether this reaction shall go forward or backward depends upon the relative amount present of the various substances entering it and upon the nature and quantity of the enzymes which bring about the reaction. She points out that certain species having flowers, leaves, etc., slightly or not at all colored give rise to colored varieties which are recessive to the type. These facts are explained if we assume that the colored forms arise because of the absence in the color tissue of the enzyme which causes the synthesis of the glucoside. Under these conditions, chromogen which is formed would be free and available for oxidation into pigment. In the type the enzyme is supposed to be present, and the condition of equilibrium is such that all, or nearly all, of the chromogen unites with sugar and hence can not be oxidized.

In the *Journal of Morphology* for March, 1911, Wilson gives a very interesting discussion of the chromosome behavior in *Nezara,* following which he gives a discussion of the possible ways in which the idiochromosomes may be changed in number.

One of the most interesting things in this paper to the student of genetics is the high degree of probability which Wilson shows to exist that the behavior of the idiochromosomes is not only accountable for sex inheritance, but for the inheritance of certain sex-limited characters. He points out that cytological considerations render it probable that the morphological dimorphism of the spermatozoa in certain species has arisen by the transformation of a single pair of chromosomes, producing an XY pair. He also shows that in certain species the XY pair of chromosomes

[1] M. Wheldale on "The Formation of Anthocyanin," *Journal of Genetics,* I, No. 2, March, 1911.

may be interpreted as an X chromosome attached to one member of a pair of Y chromosomes, thus one of the members being an XY combination, the other Y.

He then calls attention to the very interesting case of the inheritance of white eye found by Morgan in one of his *Drosophila* mutants. This mutation appeared first in the male. When this male was crossed with the normal red-eyed female the progeny all had red eyes; but in the next generation some of the males showed white eye again. Morgan has shown that in a cross of this kind it is only the female progeny which transmits the abnormality, and although she transmits it to half of both sexes of her offspring it does not appear in the female. It is possible, however, to secure females with white eyes.

These facts are all explainable on the following basis. Let WF represent the X element in which white eye is associated with the female determiner. RF would then represent the X element in red-eyed individuals. The formula for the white-eyed male would be WF.Y. The formula for the normal female is RF.RF. These mated give WF.RF females and RF.Y males; but since R is dominant to W these females have red eyes.

If now these heterozygous females be mated with ordinary males, the following four types of progeny are produced: WF.RF females, RF.RF females, WF.Y males, RF.Y males. Thus half of the males in this generation will have white eyes. But if a heterozygous female be mated with a white-eyed male, half of the female progeny and half of the male progeny will have white eyes.

Wilson points out that these phenomena exactly parallel behavior which he has found in the X and Y chromosome elements of certain species, where the X element plainly consists of an X chromosome united to a Y chromosome, while the synaptic mate is a Y chromosome. If in such a species a mutation like that of the white eye of *Drosophila* occur as a result of the loss of some characteristic on the part of the Y chromosome which constitutes a part of the X element, then such mutation would behave exactly as Morgan found this white-eye mutation to behave in *Drosophila*.

In referring to this parallel in the behavior of the chromosomes and of this mutation Wilson remarks: "So precise is the correspondence of all this with the course of sex-limited heredity of this type that it is difficult to resist the conclusion that we have before us the actual mechanism of such heredity—in other words.

that some factor essential for sex is associated in the X element with one that is responsible for the sex-limited character.''

The author points out other important parallels of a similar nature. To the cytologist probably the most interesting part of Wilson's paper is the suggestion he makes regarding the possible origin of the X and Y elements. On the whole, this paper greatly strengthens the hypothesis that there is some kind of definite relation between the chromosomes and Mendelian factors in heredity.

Doncaster, in the *Proceedings* of the Cambridge Philosophical Society[2] gives a short note on the spermatogenesis of *Abraxis grossulariata* (currant moth), in which he had previously shown that the *grossulariata* character is a sex-limited, dominant Mendelian factor, not borne by eggs bearing the female determiner. He finds the mitoses very small, and was unable to count the chromosomes satisfactorily, but says there are between fifty and sixty. Two kinds of primary spermatocytes are found, in different follicles. One of these appears to be abnormal and is thought not to be functional in fertilization. There is no evidence that the male produces two kinds (male and female determining) of spermatocytes, such as are found in many species. The number of chromosomes visible in the equatorial plate of the first spermatocyte division, as well as in the second, is twenty-eight. The oogonial mitoses do not differ recognizably from the spermatogonial.

In this moth the female produces two kinds of eggs, one female producing and wanting in the *grossulariata* character, the other male-producing and with or without this character according as the female is of the *grossulariata* or the *lacticolor* type. It is to be expected that the chromosomal provision of the two kinds of eggs would be different; yet, as Wilson and others have shown in some species for males, the differential chromosomes may not be distinguishable. Doncaster's results are consistent with the latter suggestion.

Doncaster also gives some interesting results of a test of a theory of sex inheritance which has gained considerable popular credence.[3] The theory is that one ovary produces female-producing eggs, the other male-producing eggs. The test was made on female albino rats. In one individual the right ovary was removed, in the other the left. Both females subsequently pro-

[2] Vol. XVI, Pt. I.

[3] *Journal of Genetics*, Vol. I, No. 1, November 18, 1910.

duced offspring of both sexes. Post-mortem dissection of the two females showed that the operation of removing an ovary had been entirely successful, and new ovarian tissue had not been regenerated. These results disprove the theory so far as concerns these animals.

In the March number of the *Zeitschrift für Induktive Abstammungs- und Vererbungslehre* Dr. Gates presents a very interesting paper on the inheritance of pigmentation in *Œnothera*. He shows that some quantitative variations in the pigmentation of the calyx of *O. rubrinervis* are not hereditary, while other quantitative variations are hereditary. One striking case of a mutant which produces an increased amount of anthocyanin was found in his investigations.

To most students of genetics the most interesting part of Dr. Gates's paper will be his discussion on pages 367–8 of the probable nature of the differences between genotypes which furnish us our Mendelian character pairs. The evidence he presents is strongly against the assumption that all of these hereditary differences are due to the loss or origination of definite cell organs which can be looked upon as the physical basis of the separately heritable characters. Rather, "Everything points to its being what it appears to be, namely, a positive variation in some physiological factor concerned in anthocyanin formation. It is not necessary to think of a form as having lost an inhibitor, but rather has there been a quantitative readjustment of the relation between the substances which by their chemical interactions produce anthocyanin, and those which decompose it as soon as formed, or which by their presence divert the metabolic processes and bring about chemical reactions of a different sort."

He states that the appearance and behavior of the mutant above referred to (*O. rubricalyx*) can not be explained on the basis of the presence or absence of any factor or substance in this mutant which is not also present in *O. rubrinervis*. "Obviously the germinal change has been rather in a quantitative readjustment, and it would seem that many, though not necessarily all, the cases of Mendelian color inheritance are explainable on a similar quantitative basis rather than by a presence-absence hypothesis."

He calls attention to the well-known fact that, especially in organic chemistry, many reactions may go in quite different directions according to the relative amounts of the reacting substances present, and suggests that many of the phenomena of

heredity are due to changes in the relative amounts of substances produced by the metabolic activities within the cell.

Even white varieties, which are frequently referred to as having lost the factor for color, may originate merely from a change in the quantity of some substance or substances present. That many white flowers do not owe their lack of pigment to the absence of a pigment-producing factor is shown by the fact that such flowers frequently show pigment in exceptional individuals, and many white flowers develop more or less pigment with age. Presumably, as the flower passes its prime, there may be changes in the rate at which various metabolic processes go forward, and this may induce pigment formation.

In *Science* for May 31, 1911, Professor Morgan gives some interesting data concerning the origin of a number of mutations in *Drosophila*. In a culture treated with radium one fly was produced the marginal vein of whose wings was beaded, and this character appeared in a very small proportion of the next generation. The proportion of beaded wings increased from generation to generation until a stock was produced that gives, in certain cultures, nearly 100 per cent. of the new character.

In the seventh generation of the beaded-wing stock a fly appeared with the end of the wings cut off nearly squarely, and indented at the ends, or somewhat scalloped. This character is confined almost exclusively to the female line. In the next generation twenty-one flies, with truncated wings, appeared along with 230 having normal wings. In the third generation some of the truncated-winged flies produced nearly 50 per cent. of truncated wings.

In the second generation of the beaded-wing flies a male appeared with wings shorter than the abdomen. A similar mutation occurred in a related stock. These abnormal flies bred together have produced 964 normal males and females, six short-winged males and two females.

In the seventh generation of the beaded-wing stock a fly appeared with wings like the normal in form but extending no further than the end of the abdomen. This character proves to be sex limited.

Occasionally flies have appeared, especially in the truncated-wing stock, with each wing swollen up to a balloon or a bladder filled with fluid. Practically a pure stock of this mutation is now on hand.

Several times flies have appeared that failed to develop black pigment in the body. These flies have produced no offspring.

A melanistic mutation has also occurred, and a pure stock of it was easily produced.

A male appeared in the melanistic stock having gold and yellow wings: "In fact, the entire fly is conspicuously yellow. This color proves to be sex-limited. Thus far it has appeared only in the males."

Professor Morgan has undoubtedly uncovered some new and interesting facts, and it is hoped that he will be able to discover something concerning the underlying causes of these mutations.

In *Science*, May 19, 1911, Loeb and Bancroft report experiments on the production of mutants in *Drosophila*. They secured four types of mutation; a dark form, a pink eye, a white eye, and a short-winged form. The dark form and the pink-eyed form occurred also in control cultures, and the authors think it is probable that the white-eyed mutation originated before the treatment. The short-winged mutants have appeared thus far only in cultures treated with radium, but in only two out of several hundred such cultures. The treatments used were high temperatures, exposure to radium, and exposure to Roentgen rays. Where mutations were obtained in the treated cultures they occurred in only a very small proportion of the cultures, and the authors appear to doubt whether or not the treatment was responsible for the mutations.

Professor Cockerell, in the *Annals and Magazine of Natural History*, Series 8, Vol. VII, April, 1911, describes a very interesting case in which apparently a female bee, in a genus (*Megachile*) in which the female appears to be heterozygous for the secondary sexual characters, with the female characters dominant, has lost these secondary sexual characters and assumed those of the male. He proposes a new genus (*Androgynella*) for this marked variation from allied forms. Cytological study of these two related genera might reveal something of marked interest.

I wish to draw special attention to the very able article by Professor Michael F. Guyer which appeared in this journal for May, 1911, under the title "Nucleus and Cytoplasm in Heredity." Professor Guyer in this article gives the best presentation I have seen of the relation of the various parts of the cell to the phenomena of heredity. It is not necessary to review the paper here in full, since it is available to the readers of this journal.

W. J. SPILLMAN.

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THE
AMERICAN NATURALIST

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INHERITANCE OF THE "EYE" IN VIGNA

DR. W. J. SPILLMAN

U. S. DEPARTMENT OF AGRICULTURE

CERTAIN races of the cowpea (*Vigna unguiculata*) have the seed coat completely pigmented, others have no pigment, while others have pigment confined to certain areas. In this paper the fully pigmented races are referred to as having solid color, those without pigment as white, while the pigmented area of the partially pigmented seed coats is called the "eye." This eye, when small, is always confined to the region of the hilum, and when large always surrounds the hilum. It varies widely in size and form, as shown in the accompanying illustrations, which show the principal types of eye. In *a* the pigmented area is confined to two patches on opposite sides of the hilum. In *b* the area surrounds the hilum except at its micropylar end.

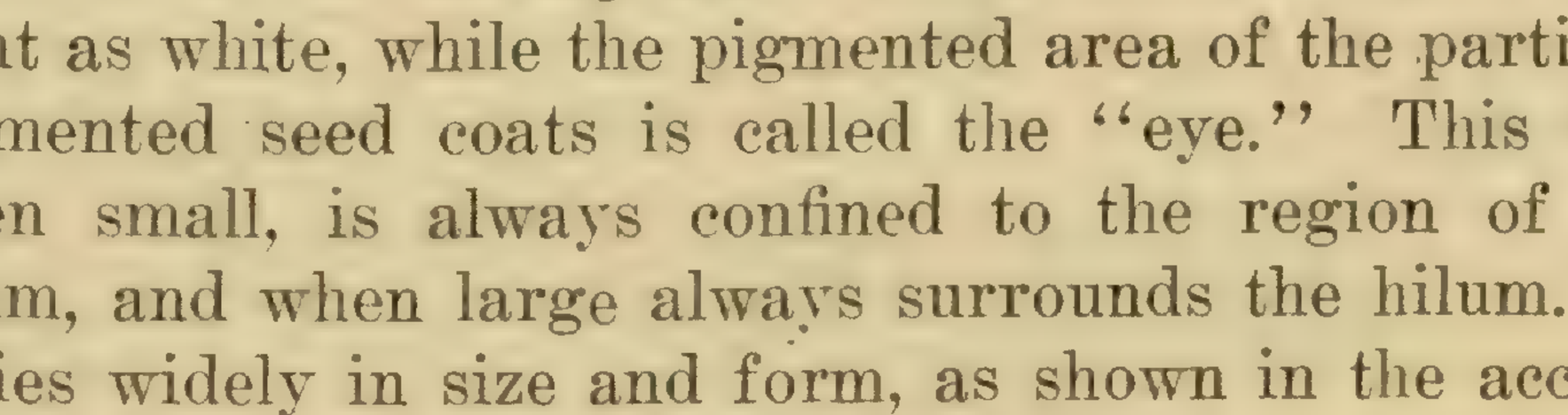

FIG. 1. Forms of the "eye," or pigment area, in the seeds of the cowpea.

In *c* the hilum is completely surrounded, but there is a broad indentation at the lower end of the pigmented area. In *d* the eye covers nearly the entire ventral[1]

[1] The terms ventral and dorsal are used in this paper to describe respectively the side of the seed showing the hilum and the opposite side.

surface of the seed, but has a characteristic notch at the micropylar end (lower end in the figure). In *e* the area has extended over the micropylar end of the seed. In this form and the next there are usually some isolated spots of pigment in the non-pigmented area. In *f* the pigmented area covers all except the dorsal portion of the chalazal end of the seed. Between the forms *a* and *f* there is nearly a complete series of connecting links represented in the material in my possession, but in the present paper I shall not attempt to deal with this whole series, because the genetic relation between some of its members is not yet worked out. Forms *a–c* will here be considered as one, under the name ordinary eye or small eye. Forms *e* and *f* will be treated as one, under the name Holstein, from the color pattern of a variety having this name. The evidence thus far available indicates that form *d*, which is here called large eye, is always heterozygous between Holstein and small eye. Perhaps other of these forms of eye are also heterozygous; material which it is hoped to obtain from the crop of 1911 (F_3) will probably determine this point. There is some evidence that forms *a*, *b* and *c* are the DD, DR and RR of a Mendelian pair. The same is probably true of *e* and *f* and a type intermediate between them. Form *g* of Fig. 1 represents a genetically distinct type of eye. In it the pigmented area surrounds the hilum, but the micropylar end of the area has the margin very indistinct; fine dots of pigment extend over the micropylar end of the seed. In races of this type that are black pigmented the pigment extends over the whole surface of the seed, but it is much denser in the region of the eye than elsewhere. The reduced pigmentation in such cases varies from very dark, rendering close inspection necessary to detect the eye, to very pale, making the eye as conspicuous as it is in buff or red pigmented races. Whether these variations in intensity of pigmentation have genetic significance is not yet determined, but investigations now in progress will, it is hoped, settle this point. This type of eye, in which an ill-defined area of pigment extends over the micropylar

end of the seed (see *g*, Fig. 1), is here called the Watson Eye, from a variety known as Watson's Hybrid, which has this type of eye. This variety, as well as the Holstein variety, is said to have originated from crosses between black varieties and Black Eye. My investigations show that both these color patterns occur in the second generation of all crosses of this kind, as will be seen later, thus confirming the supposed origin of both these varieties.

The Watson type of eye has not heretofore been recognized. But since the essential difference between it and other eye types was noticed, the writer has found in the collection of cowpea varieties in the office of the agrostologist several races having this type of eye. The existence of this type was discovered as a result of the discovery that in several crosses between eyed and completely pigmented races the ratio of fully pigmented to individuals with eyes in F_2 was 3:1 in certain cases and 9:7 in others. The latter ratio suggested that two genetically distinct types of eye were present in certain crosses. A careful study of the rather extensive material at hand revealed the types of eye already described, and a tabulation of the statistical data relating to the inheritance of each of them revealed the relations between these types which are discussed in this paper.

Statistical Data

Cross: Small Eye × *Solid Color* (fully pigmented)

In all, 21 crosses of this kind were made. In all cases F_1 was solid color. It happened that in classifying the individuals of the F_2 generation, before the types of eye present were fully recognized, Large Eye and Small Eye individuals were not separated in 5 of the 21 families. In the remaining 16 families, taken together, the proportion of the various types of color pattern in F_2 was as follows:

	Solid Color	Watson Eye	Holstein	Large Eye	Small Eye
Number of individuals in the 16 families taken together	127	41	12	34	12
Highest expectation	126	42	14	28	14

on the assumption that the ratio between these various types is 9:3:1:2:1. The reason for assuming this ratio will be given later.

In the 5 families in which the large and small eyes were not separated, and in which the corresponding expectation is the ratio 9:3:3:1, the results were:

	Solid Color	Watson Eye	Holstein	Large and Small Eye
Number of individuals in 5 families taken together	100	30	34	16
Highest expectation	101	34	34	11

In both these groups the actual numbers are in close accord with the theoretical numbers called for by the assumed ratios.

Cross: Holstein × Solid Color

Six crosses were made between various types of the Holstein pattern and solid-colored races. The F_1 plants all produced seeds that were fully pigmented. In F_2, taking the six families together, there were 75 individuals bearing fully pigmented seeds and 25 with Holstein seeds, or exactly the ratio 3:1.

Cross: Watson Eye × Solid Color

Two of the 4 Watson parents used in these matings proved to be heterozygous. The other two, taken together, gave 56 solid color and 13 Watson individuals in F_2. F_1 in all these cases was fully pigmented. The 3:1 ratio for the number of individuals in F_2 is 52:17, which agrees fairly well with the experimental results.

Cross: Small Eye × Holstein

Only one cross of this character was made. It gave F_1 with large eye; in F_2 there were 3 Holstein, 4 Large Eye and 1 Small Eye individuals, which is near the ratio 1:2:1 for these three types of color pattern.

MENDELIAN FACTORS INVOLVED

We may bring together here the various ratios found in the above classes of matings. For convenience let us designate the various color patterns as follows:

S = Solid color (fully pigmented seed coat).
W = Watson Eye.
E = Small Eye.
LE = Large Eye.
H = Holstein.

Crosses	Ratios
E × S	9:3:1:2:1 or 9:3:3:1.
H × S	3:1.
W × S	3:1.
E × H	1:2:1.

These ratios point clearly to the following conclusions:

1. Types E and S differ from each other in two factors each of which exhibits the phenomenon of dominance or partial dominance.

2. Types H and S differ in one factor which shows dominance.

3. Types W and S differ in one factor which shows dominance.

4. Types E and H differ in one factor, the heterozygote being intermediate between the parental types.

It is not difficult to formulate, in terms of the customary hypothetical factors, an hypothesis that readily explains these facts. In fact, I have been able to formulate four such hypotheses. In each of these a certain set of factors is assumed, each factor being assumed to have the power of producing a particular effect on the color pattern of the seed coat. But such explanations offer no suggestion as to the real nature and *modus operandi* of these factors. Unfortunately we do not know much concerning the complex chemical processes that go forward in the living cell. But enough is known to show that differences such as are exhibited by the various color patterns here considered may be due to some such cause as slight difference in the rate at which some enzyme may be produced in the cells of the seed coat. For instance, it is known that an enzyme may cause certain sugars and chromogens to unite to form a glucoside, thus removing the chromogen from the sphere of action of an oxidizing enzyme that might con-

vert it into pigment.[2] Another enzyme, or, under appropriate conditions, the same enzyme that brought about the synthesis of sugar and chromogen into glucoside, may hydrolyze glucoside into sugar and chromogen. It is also known that the rate at which a chemical reaction determined by an enzyme goes forward depends on the amount of enzyme present. It is therefore readily seen that the rate at which a given enzyme is produced in the cell may determine whether or not chromogen shall be available for conversion into pigment. It is also highly probable that a principal function of the chromatin of the cell is to produce the enzymes which govern at least the rate of many of the metabolic processes in the cell.[3]

It is certain that environmental conditions during ontogeny determine whether pigment shall be produced in a given tissue, even when the potentiality of pigment production is known to be present. Thus, in seeds that have pigmented coats, pigment may not occur, say in the endosperm. Causes similar to those which determine the particular tissue to be pigmented may also determine what portion of that tissue shall be pigmented. The sugar in the pigment cells of the seed coat is presumably transported there by osmosis from cells some distance away. Other materials necessary to the reactions may be brought from other parts of the organism, and some of the products of a reaction the accumulation of which might retard the reaction may be transported to other parts of the organism as they are produced. We thus have to deal with an exceedingly complex problem, many of the elements of which can not even be conjectured in our present ignorance of cell metabolism. It would therefore be idle to attempt to formulate a definite theory of the processes involved. A slight change in the permeability of certain cell walls, a change in the size of certain cells, the substitution of

[2] "On the Formation of Anthrocyanin," M. Wheldale, *Jour. of Gen.*, I, No. 2.

[3] Guyer, M. F., "Nucleus and Cytoplasm in Heredity," AMER. NAT., May, 1911.

a slightly different group of atoms for a single side chain in a molecule of chromatin or one of the constituents of chromatin, or any one of numerous other changes, might determine whether pigment is to be formed in a given cell, or whether it may be produced at all. But if the change which is responsible for the difference between two related organisms is a change in any permanent organ of the cell, then the difference in question will be hereditary. If it occurs in the material of a chromosome, or any other cell organ that behaves as a chromosome does in the reduction division, the difference in question will Mendelize.

Let us suppose, merely for purposes of illustration, that the difference between fully pigmented seed coat and the Holstein coat pattern is due to a difference in the rate at which a particular chromosome manufactures a particular enzyme under given conditions. Then when these two patterns are crossed we should get the usual phenomena of monohybridism, with the ratio 3:1 (or 1:2:1). Thus the Holstein pattern is not necessarily due to the "loss" of a "factor"; it may be due to some such cause as a difference in the quantity of an enzyme produced by a particular chromosome. The use of such expressions as "presence of a factor" and "absence of a factor" in what follows is therefore not meant to imply the presence of a morphological entity in one race and its absence in another. It rather means that in one race some cell organ, probably a chromosome in Mendelian inheritance, performs a certain function differently, or under different conditions, in the two races. Since the phenomena of Mendelian inheritance point clearly to the physical behavior of some cell organ, I prefer to think of the symbols used in expressing the genetic constitution of a type as representing the bodies, differences in the functions of which give rise to the character "pair."

Thus the symbol W in what follows may be considered as representing a cell organ which, under certain conditions, performs a certain function in such a way as to account for the difference between Small Eye and Wat-

son Eye, while w represents the same cell organ, or rather the corresponding organ, in another variety, which does not perform this same function in the same way under similar conditions. The symbol w need not imply that the power of performing any function is lost. It is here meant to imply only that the function is not performed in such manner as to produce the effect that W would have produced had it been present. Another way of putting it is that W represents a function performed, while w represents that the function is not performed. With this understanding of what is meant by a Mendelian "factor," we may proceed to examine the hypotheses which explain the statistical results given above.

The behavior of the cross: small eye × solid color indicated that these two types differ in two factors which are transmitted independently of each other. Let us represent these factors as they appear in fully pigmented peas by W and H, and in small-eyed peas as w and h. This implies, according to my conception of Mendelian factors, that some cell organ (W), probably a chromosome, performs a certain function in certain races of peas that is either not performed, or is performed differently, by the corresponding organ (w) in another race of peas. A similar remark applies to H and h. With reference to these two factors, the formula of fully pigmented peas may be written WWHH, and of small-eyed peas wwhh. We have already seen that the Holstein type differs from the type with small eye in one factor; also from fully pigmented in one factor. Hence it must have either the formula WWhh or wwHH. That is, in one of the two factors concerned it is like Solid Color, in the other, like Small Eye. We may therefore take wwHH as the formula of the Holstein type. In an exactly similar manner we arrive at the formula WWhh for the Watson type. We may bring these formulæ together for purposes of comparison.

(1)	**Solid Color**	:	**WWHH.**
(2)	**Watson Eye**	:	**WWhh.**
(3)	**Holstein**	:	**wwHH.**
(4)	**Small Eye**	:	**wwhh.**

These formulæ give the ratios previously assumed in dealing with our statistical data for the F_2 generation, provided we assume W and H dominant respectively to w and h.[4] An interesting deduction from them is that the cross between the Watson and the Holstein types should give the same ratio in F_2, namely, 9:3:1:2:1, that the cross between solid color and small eye gave. In the original crosses, the cross Holstein×Watson was not included, but it is included in crossings now being made.

These formulæ give some hint as to the nature of the effect produced by the factors W and H. Comparing (4) and (3), the factor H has the effect of enlarging the pigmented area from the small eye type to the Holstein type (see *b* and *e*, Fig. 1). Comparing (2) and (4), W is seen to have the effect of enlarging the pigmented area of the Small Eye type, changing it to the Watson type (see *g*, Fig. 1). W and H together, even in the hybrid WwHh, have the effect of spreading pigment over the whole seed-coat.

We have seen that the heterozygote between Holstein and Small Eye, which has the formula wwHh, is intermediate between the parent forms. In earlier pages this type has been designated Large Eye. It therefore appears that H duplex enlarges the pigment area about twice as much as H simplex does. Whether the same is true of the factor W has not yet been determined. As the ratio 9:3:1:2:1 is somewhat unusual, it may not be out of place to illustrate the manner of its occurrence. In the cross: Small Eye×Solid Color, F_1 has the formula WwHh, and is solid color. Generation F_2 is as follows:

F_2 OF THE CROSS SMALL EYE × SOLID COLOR. = wwhh × WWHH

		Solid Color	Watson	Holstein	Large Eye	Small Eye
1	WWHH	1	—	—	—	—
2	WWHh	2	—	—	—	—
1	WWhh	—	1	—	—	—
2	WwHH	2	—	—	—	—
4	WwHh	4	—	—	—	—
2	Wwhh	—	2	—	—	—
1	wwHH	—	—	1	—	—
2	wwHh	—	—	—	2	—
1	wwhh	—	—	—	—	1
		9	3	1	2	1

[4] The dominance is only partial in the case of H and h.

Should it later prove possible to separate the two Watson F_2 types, WWhh and Wwhh, as we can the corresponding Holstein types, we should then have the interesting ratio 9:1:2:1:2:1.

There is evidence in my material that the Holstein and Small Eye types are still further influenced by one or more additional factors. This matter is now under investigation. These additional factors appear to act in a manner entirely similar to the factor H, but have less effect. Taking the formula for Small Eye and adding a factor I, similar in effect to H, we should have the three types wwhhII, wwhhIi, and wwhhii, all three of which appear to be distinguishable, giving probably the three types *a*, *b* and *c* of Fig. 1. This point will be studied in F_3 of the original crosses, of which a vast quantity of material is growing, as well as in new crosses now being made.

OTHER HYPOTHESES

In the above hypothesis the factors W and H were assumed to have the property of enlarging the pigmented area. The facts can also be explained by assuming that w and h have the power of reducing the pigmented area. In fully pigmented races, on this hypothesis, these factors are absent. When w is introduced the pigmented area is reduced to the Holstein pattern. h, without w, reduces it to the Watson pattern, while w and h together produce the Small Eye pattern. It is necessary in this case to assume W and H dominant, respectively, to w and h, as in the first hypothesis.

We may also assume a factor W for Watson Eye, a factor, E, allellomorphic to W, for Small Eye, and a third factor, S, which tends to enlarge the pigmented area, converting Small Eye into Holstein, and Watson Eye into Solid Color. Here, W must be epistatic to E. Under these assumptions the formulæ of the principal color patterns would be:

Solid Color	:	WWSS.
Holstein	:	EESS.
Watson	:	WWss.
Small Eye	:	EEss.

A fourth hypothesis is as follows:

H = a factor for Holstein pattern.
E = a factor for Small Eye pattern.
S = a factor which enlarges the pigmented area, converting E into Watson, and H into Solid Color.
H is here epistatic to E.

All four of these hypotheses are in complete agreement with the statistical data, and lead to exactly the same types, and the same ratios, in all generations.

If we look upon the symbols as representing cell organs, differences in whose functions are responsible for the phenomena observed, then these four hypotheses are identical. They all provide exactly the same set of cell organs. The differences between the hypotheses are found only in the nature of the functions which these cell organs are supposed to perform. As we know nothing definite about these functions, the hypotheses are essentially identical within the range of present knowledge. The functions assumed for the bodies represented by the symbols of the first hypothesis seem to the writer to accord more nearly with our meager knowledge of cell chemistry.

The author desires to acknowledge his indebtedness to Mr. G. W. Oliver, who not only performed the cross-fertilizations planned by the writer, but freely made available similar extensive material of his own, which is included with my own in these studies. Mr. Oliver also grew the F_1 hybrids. He is also under obligations to Mr. J. W. Froley, Mr. E. D. Carmack and Mr. W. R. Humphries, who grew the F_2 plants and made the necessary field notes; to Mr. E. P. Humbert, who rendered valuable assistance in classifying the F_2 material, and to Professor C. V. Piper, agrostologist of this bureau, who furnished seeds of the varieties used as parents in these investigations, and made many helpful suggestions concerning probable "factors" present in the varieties.

HEREDITY OF HAIR FORM AMONG THE FILIPINOS

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WHILE connected with the Philippine Medical School in Manila, in the year 1909 two of my pupils, Maria P. Mendoza and Manuel Ramirez, became interested in the heredity of hair form through the work of Gertrude C. Davenport and Charles B. Davenport[1] and they collected the records of 36 families, largely Chinese-Tagalog crosses, although two families were Negritos who had married Filipinos.

They tested the hair form by making sections of hair dipped in thick celloidin hardened in 70 per cent. alcohol and cross-sectioned with a hand microtome, after which the sections were examined under the low power of the microscope, the measurements being made with an ocular micrometer. They divided the forms of hair into—

Straight, with diameters of 100 : 90 or over,
Wavy, with diameters of 100 : 70–90,
Curly, with diameters of 100 : 60–70.

They decided that wherever a union occurred between individuals with straight and wavy hair the straight hair predominated. It seems expedient, however, to consider the hair form in single families as well as *en masse*.

In any discussion of heredity it seems necessary to consider individuals rather than the mass, except in the formulation of laws that take into consideration probable errors in the mass. In Table I, showing the result, in mass, of crossing different hair forms, we should expect, if Mendel's laws prevail, where wavy and straight are crossed or where curly and straight are crossed, to get an equal number of offspring with straight and curved hair

[1] AMERICAN NATURALIST, Vol. XLII, April, 1908.

TABLE I

COMPILED BY MENDOZA AND RAMIREZ

No.	2d Parental FF FM	2d Parental MF MM	Parent F M	Children C	Children W	Children S	Nature of Mating		Expectation C	Expectation S
1	W / S	S / S	W / S	3	1	1	DR	R	2.5	2.5
2	=	=	W / S		3	4	DR	R	3.5	3.5
3	=	=	S / S	3		3	R	R		6
4	=	W / S	S / W	1	5	2	R	DR	4	4
5	=	W	S / W		1	1	R	DR	1	1
6	S / S	S / S	S / S	1		2	R	R		3
7	=	C / S	S / C	1	0	2	R	DR	1.5	1.5
8	C / C	W / W	C / W	6	1	0	DR	DR	5.3	1.7
9	S / S	S / S	S / W	1		1	R	DR	1	1
10	C / S	S / S	W / S	4	1	2	DR	R	3.5	3.5
11	C / S	S / S	S / S		1	1	R(?)	R		2(?)
12	C /	C / C	C / W	2		1	DR	DR	2 3	.7
13	/	W / S	W / S	2	2	1	DR	R	2.5	2.5
14	C / W	S / S	C / S	2	1	1	DR(?)	R	2	2
15	C / W	S / S	C / S	1	1	1	DR	R	1.5	1.5
16	C / W	S / S	C / S	2	1	1	DR	R	2	2
17	= / S(C)	K / K	S(C) / K	4			DR	DR	4	0
18	S(C)	S / S	S / C			3	R	DR	1.5	1.5
19	S	S / S	S / S			8	R	R		8
20	S	S / S	S / S			4	R	R		4
21	S	S / S	S / S			6	R	R		6
22	S / W	= / W	S / W	2	4	1	DR	DR	5.3	1.7
23	S / S	C / C	S / C	1	1	1	R	DR	1.5	1.5
24	S / S	=	S / W	1		3	R	DR	2	2
25	S / S	=	S / W			5	R	DR	2.5	2.5
26	S / S	S / C	S / C	1		5	R	DR	2.5	2 5
27	S	C / S	S / C			3	R	DR	1.5	1.5

No.	2d Parental FF FM	2d Parental MF MM	Parent F M	Children C	Children W	Children S	Nature of Mating		Expectation C	Expectation S
28	S C	S S	S C	1		2	R	DR	1.5	1.5
29	C C	S S	C S	2		1	DR	R	1.5	1.5
30	S S	=	S C	2		3	R	DR	2.5	2.5
31	S S	S S	S W	1	1	4	R	DR	3	3
32	K K	S S	K S		4		DD	RR	4	
33	=	=	C S	2	1	1	DR	R	2	2
34	=	=	W S	1	1	5	DR	R	3.5	3.5
35	=	=	W S	1	3	2	DR	R	3	3
36	=	S S	S W	1	2	3	R	DR	3	3
37	S y	W C	W C	3		2	DR	DR	3	1.25
38	S S	W W	S W		3	7.	R	DR	3.5	3.5
39	=	S C	S C	3			R	DR	1.5	1.5
40	=	=	S C	1	1	1	R	DR	1	1
41	3	S C	W S	1	5	6	DR	R	6	6
42	=	=	C C	2			DR	DR	1.5	.5
43	S	C S	W W	1	1	2	DR	DR	3	1
44	W C	S W	W W	2	1	2	DR	DR	3.7	1.25
45	=	C	S C	2		8	R	DR	5	5
46	=	C S	S W	3		4	R	DR	3.5	3.5

F = father, M = mother, D = dominant, R = recessive, S = straight, W = wavy, C = curly, K = kinky.

where the curved variety is a dominant heterozygote and the straight is a recessive homozygote. Such is the case, for of the 31 families examined in which wavy is crossed with straight or curly with straight, there are 157 children of whom 84 have straight hair and 73 have hair curly or wavy. Where the wavy and the curly are crossed, if each is a heterozygote with the straight recessive, we should expect to find three children with the curved

proportion, for of the five families where wavy hair is crossed with curly, there are 33 children with hair of the curved variety and eight with straight hair.

When individual families are considered, however, there seems to be an alteration of the dominance in some cases. Straight hair is dominant in some families, whereas in others the wavy or curly is dominant. In Table I straight hair appears to be dominant in the families numbered 3, 6, 11, 18, 24, 25, 26, 27, 31, 34, 38 and 45. In the first three of these families where both parents have straight hair, and particularly in family 6, curly hair is evidently recessive. If the gametic composition of the two parents in family 3 is Dr×Dr, in which D = straight hair dominant and r = curly hair recessive, then the expected proportion of offspring would be 3 straight to 1 curly haired child. The number of curly-haired children is 3 instead of 1, which is greater than it should be. But if the straight hair be recessive in this family, the gametic composition must be rr×rr where r is straight recessive, and all of the children should have straight hair, which is not true. In any case the number of curly-haired children is in excess of what it should be.

The curved form of hair seems to be dominant in a greater number of families than is the straight, as in families numbered 1, 4, 10, 12 to 16, 22, 28, 29, 33, 35, 36, 39, 41, 43 and 44. In family 1 the proportion of curly-haired children is in excess (excessive dominance) of what it should be even though the curved be dominant. The same is also true for families 4, 10, 13 and 39. There is, on the other hand, imperfect dominance (recessive dominance) of the curved hair in families 14, 15, 16 and 29; or, in other words, there are fewer children with curved hair in these families than would be anticipated if the curved form be dominant.

When kinky hair and straight hair are crossed, as in families 17 and 32, there results an intermediate form—in one family all the children have curly hair, in the other all have wavy hair. The result of crossing two of these

intermediate forms is not known unless such a cross is represented by families 8, 12, 22, 37, 42, 43 and 44. There is a tendency toward segregation in these families, but no kinky hair appears.

Judging from this cursory analysis of the families under consideration, the inferences are that in the crossing of different grades of hair-form there is a tendency towards segregation or alternate heredity, a modified Mendelism, for there is not a perfect dominance, nor the opposite, for either of the extreme grades of hair form, kinky (woolly) or straight.

It would be of interest to know what relationship the curly, wavy or kinky hair of the European bears to the same sort of hair of the Negrito. Presumably all of the curly or wavy hair in the families under consideration is of European origin except in families 17 and 32 of Negritos, but in no instance can the previous inclusion of Negrito blood be absolutely excluded. Some of the wavy or curly hair may therefore be due to previous crosses of the Filipino and Negrito. Presumably, also, all of the straight hair is derived from the Filipino, but again the European or Chinese straight hair can not be excluded. It may be that the straight hair of the Chinese and of the European would each have a different reaction in heredity with the curved variety of both the European and the Negrito. Unfortunately, observations to determine this may not be possible owing to the mixed condition of the population at the present time.

It may be well to tabulate the families in which the parents are alike and unlike in hair form and to note the kind of hair of the children, in order to determine somewhat exactly the relative behavior of the different forms of hair in heredity. The following crosses will be considered: Group I, straight×straight; group II, curly× curly; group III, wavy×wavy; group IV, straight× curly; group V, straight×wavy; group VI, curly×wavy.

In this and subsequent tables F. = father, M. = mother. C. = curly. W. = wavy, S. = straight, F.F. =

TABLE II

GROUP I, STRAIGHT × STRAIGHT

No.	F.F.	F.M.	M.F.	M.M.	Children			Parents	
					C.	W.	S.	F.	M.
3	—	—	—	—	3		3	S	S
6	S	S	S	S	1		2	S	S
11	C	S	S	S		1	1	S	S
19	S	S	S	S			8	S	S
20	S	S	S	S			4	S	S
21	S	S	S	S			6	S	S

father's father, F.M. = father's mother, M.F. = mother's father and M.M. = mother's mother.

Here are three families (3, 6, 11) in which the parents appear to be simplex or heterozygotes, and three (19, 20, 21) in which they appear to be duplex or homozygotes, and the straight hair is dominant to the curved variety. The parents in the first three families would have a gametic composition of Dr×Dr in which D represents the dominant character, straight hair, and r represents the recessive, curved hair. In any cross of this nature an equal number of children with straight hair and with the curved variety would be expected and the expectation is realized. The parents in the second three families would have a gametic composition of DD×DD, where D represents the dominant character, straight hair, and only straight-haired children should result from such unions. The gametic composition of the last three families could be rr×rr, where r is recessive straight hair, but if straight hair acts as the dominant character in the first three families there is no reason to suppose that it would be recessive in the last three.

TABLE III

GROUPS II AND III, CURLY × CURLY AND WAVY × WAVY

No.	F.F.	F.M	M.F.	M.M.	Children			Parents	
					C.	W.	S.	F.	M.
42	—	—	—	—	2			C	C
22	—	W	—	—	2	4	1	W	W
43	—	S	C	—	1	1	2	W	W
44	W	C	S	W	2	1	2	W	W
Total					7	6	5		

Family 42 is apparently duplex or homozygote with a gametic composition of cc×cc, but there is nothing to indicate whether the curly hair is dominant or recessive. The wavy haired families behave as if simplex or heterozygote, producing both straight and curly-haired children. If wavy hair is produced by a combination of straight and curly it should behave as it does, representing the heterozygote of the F^1 generation, and in the next generation (F^2) there is a return of the two original forms of hair, curly and straight, and a continuance of the wavy.

TABLE IV

GROUP IV, STRAIGHT × CURLY

No.	F.F.	F.M.	M.F.	M.M.	Children			Parents		Children		
					C.	W.	S.	F.	M.	C.	W.	S.
7	—	—	C	S	1		2	S	C			
14	C	W	S	S				C	S	2	1	1
15	C	W	S	S				C	S	1	1	1
16	C	W	S	S				C	S	2	1	1
18	S (C)	S	S	S			3	S	C			
23	S	S	C	C				S	C	1	1	1
26	S	S	S	—	1		5	S	C			
27	S	S	C	S			3	S	C			
28	S	C	S	S	1		2	S	C			
29	C	C	S	S				C	S	2		1
30	S	S	—	—	2		3	S	C			
33	—	—	—	—				C	S	2	1	1
39	—	—	S	C				S	C	3		
40	—	—	—	—				S	C	1	1	1
45	—	—	C	—	2		8	S	C			
Total					7		26			14	6	7

In some straight×curly families, curly hair seems to be dominant, as in 14, 16, 29, 33 and 39. Whereas in others straight hair seems to be dominant, as in 7, 18, 26, 27, 28, 30 and 45. It will be noted that whatever the character of the father's hair, that character is dominant except in family 39. It is also to be noted that straight hair is dominant when three of the grandparents have straight hair, whereas curly hair is dominant when only two of the grandparents have curved hair. If the hair form of the dominant parent is duplex no recessives are to be expected, but if the dominant parent is simplex half

of the children will have little or no dominant hair form. Neither of these expectations is met, except in the families where curly hair appears dominant and there the latter hypothesis fits the facts—14 children have curly hair, 13 have not. We may be dealing with a case of dihybridism in which there is one masked character.[2] The two pairs of characters may be: straight dominant to its absence (curly), and straight dominant to wavy. We should expect on this supposition to get straight, wavy and curly in the proportions: straight 9, wavy 3 and curly 4. The actual number of children with the different kinds of hair is straight 33, wavy 6 and curly 21.

The results of crossing straight and wavy hair may profitably be considered at this point.

TABLE V

GROUP V, STRAIGHT × CURLY

No.	F.F.	F.M.	M.F.	M.M.	Children			Parents		Children		
					C.	W.	S.	F.	M.	C.	W.	S.
1	W	S	S	S				W	S	3	1	1
2	—	—	—	—		3	4	W	S			
4	—	—	W	S				S	W	1	5	2
5	—	—	—	W		1	1	S	W			
9	S	—	—	S	1		1	S	W			
10	C	S	S	S				W	S	4	1	2
13	—	—	S	W				W	S	2	2	1
24	S	S	—	—	1		3	S	W			
25	S	S	—	—			5	S	W			
31	S	S	S	S	1	1	4	S	W			
34	—	—	—	—	1	1	5	W	S			
35	—	—	—	—				W	S	1	3	2
36	—	—	S	S	1	2	3	S	W			
38	S	S	—	W		3	7	S	W			
41	—	S	S	C				W	S	1	5	6
46	—	—	C	S	3		4	S	W			
Total					8	11	37			12	17	14

The father is again prepotent, but there are more exceptions in the straight×wavy cross than in the straight ×curly cross. A great many more curly-haired children (20) appear in the former than wavy-haired children (6) in the latter. The additional factor of dominance associated with the male parent should be noted.

[2] "Mendelism," by R. C. Punnett, Cambridge, 1907, pp. 44–52.

Davenport and Davenport[3] have apparently overlooked the fact that the mother rather than the father seems to favor dominance in the American families in which the hair form is recorded by them. When the mother has straight hair in a cross of curly and straight, the number of children is 4 curly to 24 straight, but when the mother has curly hair in a similar cross, the number of children is 10 curly to 22 straight. It may be significant that in America, where curly hair is dominant and straight recessive, the female parent is associated with dominance, whereas in the Philippines, where straight hair is dominant and curly recessive, the male parent is associated with the dominant hair form.

It is to be regretted that no observations as to the sex of the children were made by either Davenport and Davenport or Mendoza and Ramirez, because if that had been done the repulsion of maleness or femaleness to one form of hair or another might have been determined, in view of similar conditions that exist in the currant moth and in canaries.[4] It appears, however, that femaleness exerts a repelling influence upon the dominant character among Filipinos but maleness exerts the same influence among Americans.

Returning to the cross of straight and wavy hair, it is to be noted that if straight hair is duplex and wavy hair simplex, then the supposition is that half the offspring shall have straight hair and half wavy hair, and there shall be none with curly hair. But if straight and wavy hair represent two different stages of hair-form either of which may be epistatic to curly, then a certain proportion (usually more than 25 per cent.) of the offspring should have curly hair. Actually there are many children with curly hair (a little over 25 per cent. of all offspring) and consequently the second supposition is favored.[5] We

[3] *Op. cit.*

[4] "Mendelism and Sex," by C. C. Hurst, pp. 1–34, an address delivered to the Mendel Society, March 29, 1909.

[5] Cf. Davenport and Davenport, "Skin Pigmentation in Man," THE AMERICAN NATURALIST, Vol. XLIV, No. 527, November, 1910.

may suppose that the gametic composition of the wavy hair is that of the intermediate form between curly and straight, a heterozygote, cs, and that half of the straight hair is simplex, Sc, and half is duplex, SS. The result of mating curly and straight hair would be offspring in the proportion and with the gametic composition of 2SS-straight hair, 1cc-curly hair, Ics-wavy hair, and this proportion is approximately the truth. There are in Table V 51 children with straight hair, 20 curly-haired, and 28 wavy-haired children.

Only three families occur with a cross of curly and wavy hair. Therefore no conclusions may be safely drawn from them. The curly hair does appear to be dominant in these families, and the straight hair recessive, however, because there are 11 curly-haired children, 3 straight-haired, and 1 child with wavy hair.

The two Negrito families where kinky, or woolly, hair is crossed with straight, have four children with curly hair in the family where one grandmother probably had curly hair, and four children with wavy hair where no such presumption exists. There can be no doubt that in a cross of straight and woolly hair the hair-form blends in the first generation. Curly and wavy hair appears wherever the Negrito and the Malay have been in contact for any length of time in the Philippine Islands, and especially among those who are called Negritos, as the Bataks of Palawan, the Negritos in Mindoro, Panay, Zambales, Cagayan and among the Ilongots. Inferences from the present study are that straight hair predominates in families where the ancestry has a predominance of straight hair. Therefore, the inverse of this should be true, namely, that woolly hair should predominate where the ancestry shows a predominance of woolly hair. This question might be decided by records from Negrito families where both parents have wavy or curly hair. The dominance of straight hair over curly has been indicated in previous studies by the author as in the proportion of

84 straight-haired to 24 curly-haired Filipinos of the Primitive type.[6]

To compare the results obtained from the previous records they may be assembled in one table.

TABLE VI

THE DISTRIBUTION OF THE HAIR AMONG THE CHILDREN OF DIFFERENT MATINGS

Mating	Occurrence				Relative Proportion		
	Total	Curly	Wavy	Straight	Curly	Wavy	Straight
Curly × curly	2	2			100		
Curly × wavy	15	11	1	3	73.3	6.6	26.6
Curly × straight	60	21	6	33	35.0	10.0	55.0
Wavy × wavy	16	5	6	5	31.2	37.6	31.2
Wavy × straight	99	20	28	51	20.2	28.3	51.5
Straight × straight	29	4	1	24	13.8	34.5	82.7
Kinky × straight	8	4	4		50.0	50.0	
Total	229	67	46	116	29.2	20.1	50.7

Three classes may be segregated, taking the relative proportions of curly hair alone. In the first class neither parent shows the dominant character and 100 per cent. of the children have curly hair, which would be anticipated from Mendelian crosses of R × R. In the second class only one parent shows the dominant character and the curly-haired children constitute approximately 50 per cent.—curly×wavy 78 per cent. and curly×straight 34 per cent.—which would be anticipated from Mendelian crosses of R×DR. In the third class both parents show the dominant factor and the curly-haired children constitute approximately 25 per cent.—straight×straight 12 per cent., wavy×straight 20 per cent., wavy×wavy 40 per cent., which is to be expected from DR×DR matings. The proportions are not exactly those to be expected if the straight hair is dominant, due no doubt to the small number of individuals observed, but a tendency towards dominance on the part of straight hair and recessiveness on the part of curly hair is to be noted. Some discord-

[6] Filipino Ears, this journal, Sec. A, Vol. IV. No. 1. January. 1909. pp. 27–53.

ance in the proportions may be due to the fact that when the father has curly hair and the mother straight, the curly hair is dominant, while at other times it acts as a recessive. The fact that 46 families have 47 parents with wavy or curly hair and 45 parents with straight hair, and 113 children with wavy or curly hair and 116 with straight hair indicates that either the curved or the straight may be dominant unless curly and wavy are separable forms, in which case, straight hair should be considered dominant. There are, however, twice as many known straight-haired grandparents as there are curly- and wavy-haired combined. Curly and wavy hair seem to have been latent (recessive) in the grandparents, and predominance of straight hair in the ancestry may make straight hair dominant in heredity.

Summary

There can be no doubt that hair form blends in heredity when different forms are crossed, and there can also be no doubt that segregation of hair form occurs to some extent in heredity, and one form or another may be dominant under different conditions. There is no exact conformity to Mendel's laws, although there is a tendency in that direction.

There is evident potency in the male when curly and wavy hair are crossed: when the father has curly hair, that form is dominant, and when the father has straight hair, straight is dominant. Wavy hair seems to be a blend of curly and straight in the condition of a heterozygote, each of the two forms, curly and straight, reappearing when the parents are wavy-haired. Wavy hair is epistatic to curly and hypostatic to straight; it may carry hypostatic curly while straight may carry either hypostatic curly or hypostatic wavy. There is evidence of unusual activity of the curly determiner, in spite of the fact that curly hair is usually recessive among the Filipinos.

In conclusion the results observed for Filipinos are

not the same as the results recorded by Davenport and Davenport in America but, in general, they are the reverse. When two curly-haired Filipinos are united in marriage the chances are that all their children will have curly hair. Two wavy-haired parents may have straight, wavy or curly-haired offspring. Two straight-haired parents may have children with either straight, wavy or curly hair and the proportion of straight-haired children will probably be large. When one parent has curly hair and the other straight, the greater part of the offspring will have straight hair if the father's hair is straight, but if the father's hair is curly, the proportion of curly-haired children will be larger. But the families of straight- and wavy-haired parents will probably have curly as well as straight and wavy hair, for waviness is usually heterozygous.

Note.—Wherever I may have used the construction and wording previously used by Davenport and Davenport, it was done to emphasize the fact that the results of the observations on the hair-form of the Filipino are different from those found by the two authors in America. I have reversed the terms in applying their language to the facts.

A large number of records would be desirable, both of Filipinos and of Europeans, and records of Negrito and Malay or Negro and European would be especially desirable. The hereditary reactions of different kinds of straight and curly hair may differ, but this could be determined only by more numerous records. Let us hope the records will be forthcoming.

THE ZOOGEOGRAPHY OF THE EAST INDIAN ARCHIPELAGO[1]

DR. P. N. VAN KAMPEN

TRANSLATED FROM THE DUTCH BY

THOMAS BARBOUR

TRANSLATOR'S NOTE

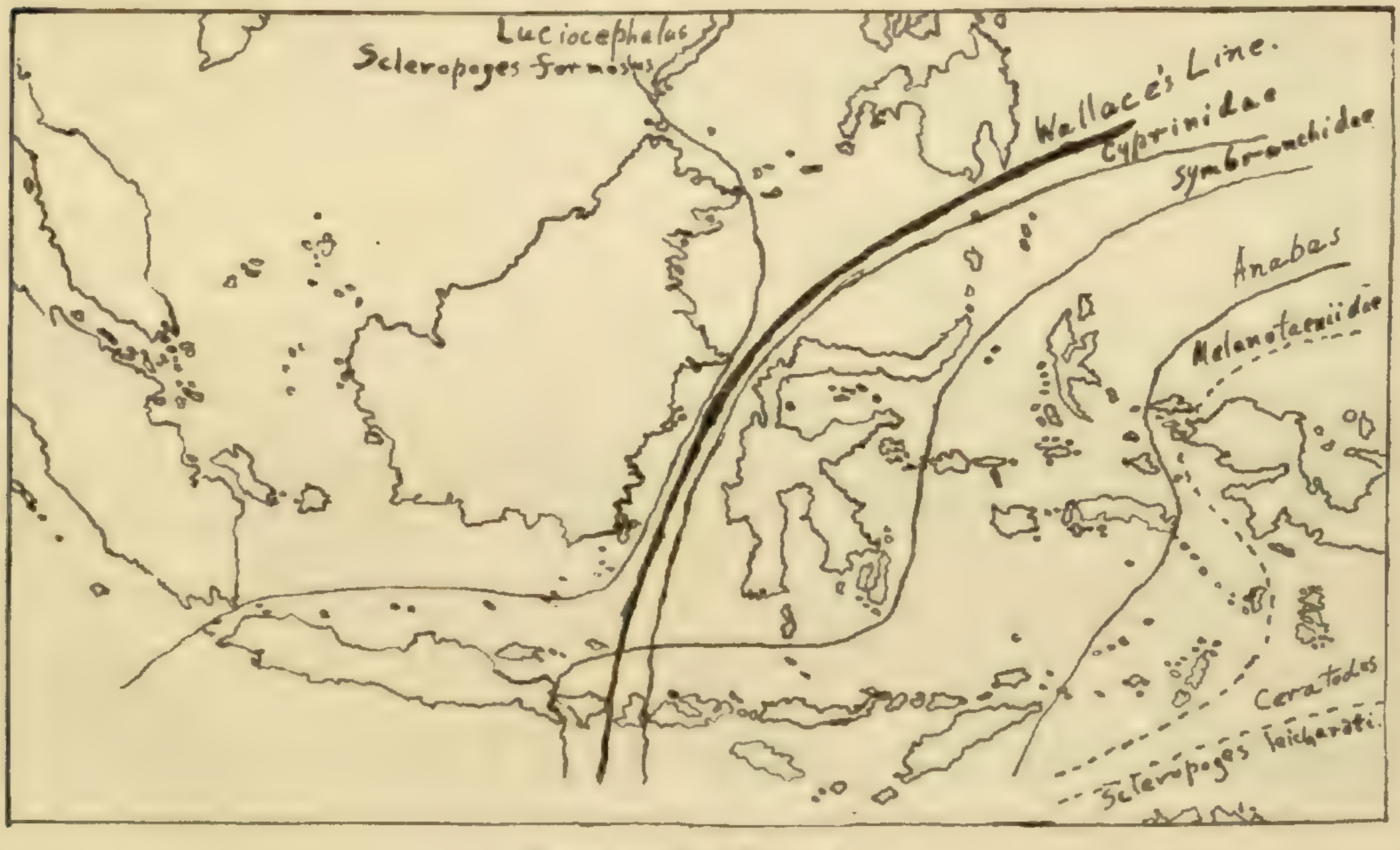
NEARLY a year ago I received from my friend Dr. van Kampen a paper which seemed at once of such present interest and general excellence that I believed it should be made available for English-speaking students of zoogeography. Its original publication in Java makes it inaccessible to many. The essay was written to be read before the Debating Club of the Batavian Royal Natural History Society; and I am under obligation to both Dr. van Kampen and the president of the Koninklijke Natuurkundig Vereeniging for permission to make and publish this translation.

THE ZOOGEOGRAPHY OF THE EAST INDIAN ARCHIPELAGO

Even a superficial examination shows us that a very considerable faunistic differentiation exists between the western and eastern halves of the Indo-Australian archipelago. Perhaps this differentiation is most evident amongst the mammals. If one compares, for instance, Sumatra with New Guinea, one finds at once upon the first-named island a number of large mammals, such as the tiger and the leopard, the rhinoceros and the tapir, which are of course unknown upon New Guinea. Here, on the other hand, certain marsupials are found, as well as the strange egg-laying ant-eaters, of which there is no sign upon Sumatra. One finds similar phenomena upon

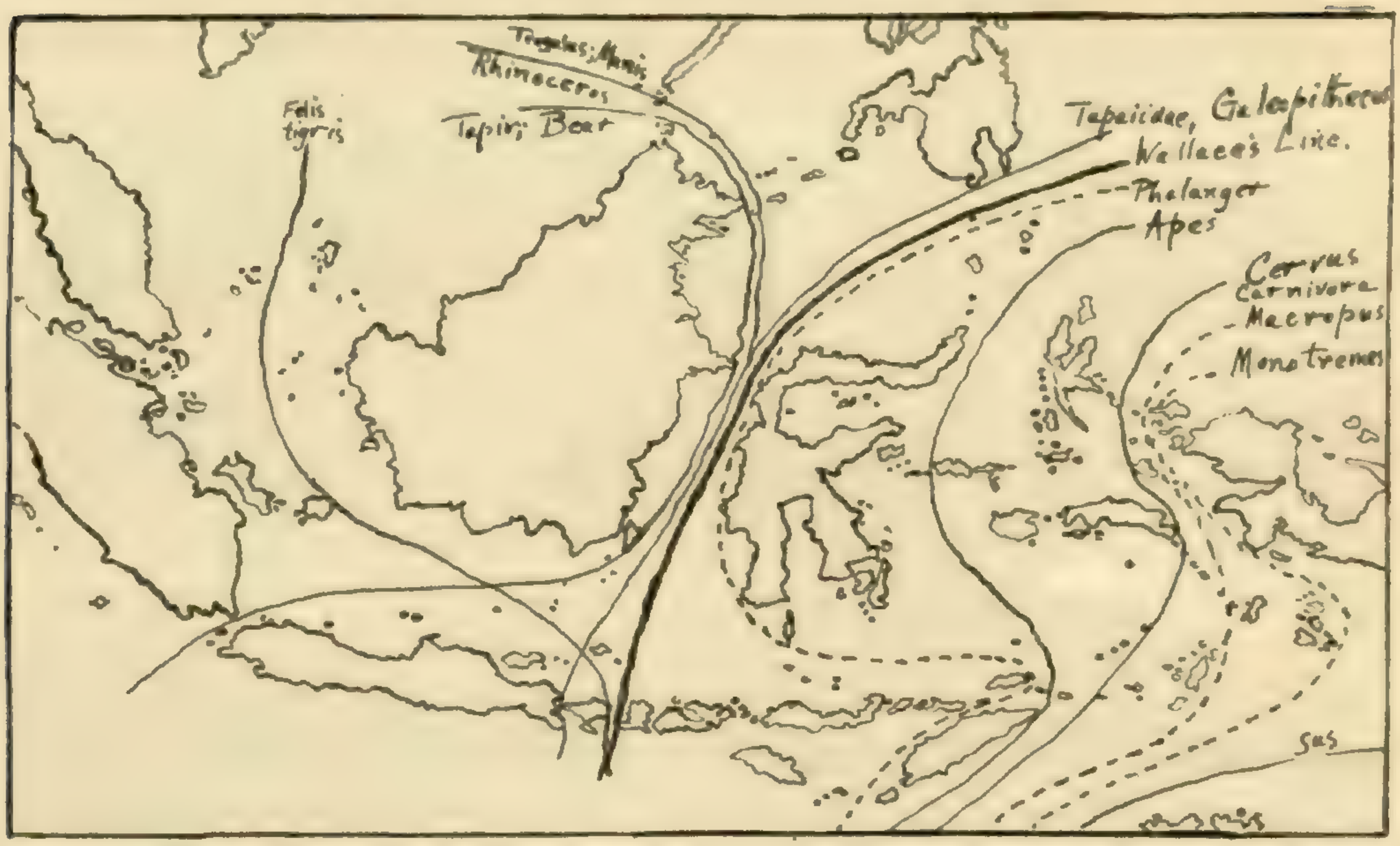
[1] Original title: "De Zoogeografie van den Indischen Archipel door Dr. P. N. Van Kampen. Overgedrukt uit Bijblad No. 3 en 4 van het Natuurkundig Tijdschrift voor Nederlandsch-Indië." Weltevreden, Boekhandel Visser & Co., 1909.

studying most of the other groups of animals. Faunistic differences comparable to these which we have here mentioned for the Indian archipelago are naturally found in other regions of the world. It is not long ago that zoologists gave little or no consideration to these phenomena of distribution, but simply busied themselves with describing hundreds of new species without caring whence these species came. It was only at the beginning of the nineteenth century that a change came about.



Freshwater Fishes.

Amphibians.



Mammals.

Explanation of the Map

On the map are given the easterly boundaries of a number of Indian groups of animals, shown by continuous line; and the westerly boundaries of some Australian forms, shown by broken lines. Map No. 1 is based on fresh-water fishes; No. 2, upon amphibians; No. 3, upon mammals. On all three maps, Wallace's line is shown as an extra heavy one; and it will be seen by comparing this with the lines bounding the ranges of other classes that it has no value as a zoogeographic boundary. The Indian animals in very many cases reach to the eastward of it, while the Australian forms do not reach out to it, so naturally do not cross it. One sees at once that the Indian and Australian components of the fish fauna are widely differentiated; and that among amphibians and mammals it is necessary to take nearly the entire eastern half of the archipelago as the transition region which we have mentioned before.

They then began to divide up the earth into a larger number of "kingdoms," by separating one fauna from another according to its similarities or differences.

These divisions differed not alone according to their originators, but also greatly in accordance with the group of animals upon which they happened to be based. Finally, it became generally agreed that Wallace, the founder of the zoogeography of the present day, had found a division which held for all land animals. That this opinion was in reality incorrect will be shown later on.

The divisions proposed by Sclater date from about 1858. Founded on the distribution of birds, it has been held by almost everybody up to the present time as covering the distribution of birds and mammals. This division of the earth is, with a few minor changes, as follows:

1. *Palæarctic Region.*—Europe; the greater part of Asia; Africa to the north of Atlas and Sahara.

2. *Ethiopian Region.*—Africa to the south of the Sahara; Madagascar and the neighboring islands; South Arabia.

3. *Indian or Oriental Region.*—India to the south of the Himalayas; south China; the western portion of the Indian archipelago.

4. *Australian Region.*—Eastern portion of the Indian archipelago; Australia; New Zealand; Polynesia.

5. *Nearctic Region.*—North America as far as northern Mexico.

6. *Neo-Tropical Region.*—Southern Mexico; the Antilles; South and Central America.

The subdivisions of these regions need not be taken up in more detail here. But it should be mentioned that Huxley in 1868 proposed the name of Notogæa for the Australian and Neo-tropical regions taken together as contrasted to the others, which he combined under the name of Arctogæa.

Zoogeography deals not alone with the question of how animals are spread over the face of the earth, but

rather attempts to explain the reasons for the peculiarities of their distribution. At first men sought the explanation especially in climatologic factors, or else they considered each zoogeographic region to be a particular center of special creation. Finally the theory of evolution in this, as in so many other subjects, spread a new light. Zoogeography has become, then, especially since it came under the leadership of Wallace, an essentially historical study.

Every type of animal has come into existence upon some specially circumscribed part of the earth, and has spread itself thence over a greater or lesser extent of surrounding territory. Only very seldom does it happen that one spreads itself over the whole earth or even a considerable part of it; the great majority are hindered by unsurmountable obstacles, and inhabit only a limited region. Zoogeography, then, on the one hand, must deal with the means of dispersal, and on the other hand with the hindrances which species may encounter.

These obstacles are, in general, spoken of as being of a climatic or orographic nature. The latter are not surprising; for if the surface of the earth were homogeneous in character, then the animals would naturally have distributed themselves in girdles or zones at even distances from the equator. Indeed, this is to a considerable extent the case with the marine fauna, against the spread of which such hindrances as we have mentioned play a minor rôle. Thus we can differentiate and recognize an arctic, a circumtropical, and an antarctic zone (Ortmann). The Indopacific Ocean, obviously belonging to the circumtropical belt, is faunistically a single entity, and to this our archipelago belongs.

While in earlier times climate and natural conditions were held as being most answerable for differences in land and fresh-water faunas, they far more slowly took the orographic factors at their true value; though naturally the first-named influences must not now remain unheeded.

Great deserts, high mountain ranges, and extensive

bodies of water are all impassable to most land animals. We can not then wonder that the fauna of North Africa is sharply differentiated from that which lies to the south of the Sahara; and so also that the Himalayas form a boundary between two zoogeographic kingdoms.

How, now, are we to explain the cases where two similar faunas are separated from each other by what seems to be a similarly impassable barrier? How is it possible, to draw an example from our own archipelago, to make comprehensible the fundamental similarity of the fauna of Sumatra and of the Malay Peninsula? In this case only two possibilities are thinkable: either by some means or other the animals have been able to get across the sea, by flying or swimming, by the aid of wind or drift-wood, or through transport by human agency; or else there has been an earlier land connection which has now completely disappeared.

Above all others this last mentioned explanation is the most fruitful for further investigation, as in general it involves calling to aid geologic factors to elucidate the reason for zoogeographic evidences of differentiation. To Wallace belongs the credit of having brought to light the true import of these factors. Zoogeography, then, may now be considered as a science auxiliary to geology.

It is evident after stating the foregoing premises that it is quite impossible to divide up the earth into sharply defined areas of distribution which hold alike for all groups of animals. Different groups owe their spread over the earth to different reasons. Some may pass easily over mountains; others (notably birds) may as easily cross the sea; some are far more dependent upon climate and the condition of the ground on which they exist than others; the oldest groups of animals, speaking geologically, have had far more time to distribute themselves than have the younger; etc. We must, however, confess that, following in the footprints of Wallace, perverted conceptions have long held sway regarding the Indian archipelago.

As to the worth of zoogeographic data in explanation of these phenomena of dispersal, we must consider the frequent impossibility of gathering all the evidence bearing on the subject. This is not the place to do more than set forth in merest generality the justification for the assertions made in the following outline. These drawbacks, moreover, surely should not hinder us from continuing, with careful circumspection, to compare most inquisitively all the available facts, being certain that many important conclusions will be reached in the end. In this manner I purpose to give here a review of that which has already been learned regarding the Indian Archipelago.

The Indo-Australian Archipelago is, from a zoogeographic point of view, a region of the highest importance. It owes this special prominence to its lying upon the boundary of two great kingdoms, the Indian and the Australian, which show a greater faunistic differentiation between one another than the rest of the old world.

Sal. Müller first noticed this difference which exists between the western and the eastern portions of the Archipelago; and, following the teachings of his time, he laid this distinction to the influence of climate and natural conditions; so that while the western half has a purely Indian character, the eastern portion—the islands of which, generally speaking, are smaller—form an area of transition to the conditions which obtain in Australia. Müller in his conclusions came in reality nearer to the present opinion than did Wallace; but the real, underlying causes of the differences remained, of course, hidden from him. The boundary between both regions he drew through the Straits of Macassar, and in the south between the islands of Sumbawa and Flores; while with some doubts he placed the island of Mindanao in the eastern, and the remaining Philippine islands in the western, section of the group.

The first to bring geologic explanations to aid in explaining the faunistic differences between the eastern and the western parts of the archipelago was Earl. But

Wallace was the foremost really to back up his opinions with valid evidence in setting forth the theory which has proved so pregnant with suggestion.

Wallace, who made long journeys among the islands, was the discoverer of the famous "Wallace's Line," as it was named by Huxley, which still, to the present day, is carefully explained in many text-books; though in reality it is disproved, and Wallace himself is not so sure of its existence during the later years of his life.

According to Wallace's original opinion, based especially upon the distribution of mammals, birds and insects, he saw a sharp faunal boundary that could be drawn through the archipelago, which ran to the eastward of the Philippines, continued between Borneo and Celebes, and on between Bali and Lombok. The fauna to the west of this line was said to be Indian; to the east, Australian. Wallace's dictum is well known, that the faunas of Bali and Lombok are more sharply differentiated from one another than those of England and Japan.

Wallace sought the explanation of these phenomena in the fact that the western half of the archipelago had in earlier times been connected with the Indian mainland, the eastern islands with Australia; and that they remained joined together until they were divided by narrow arms of the sea. The exceptions which existed Wallace explained in part through transport across water, part as their being remains of the earliest fauna which had lived upon the old land connection between Asia and Australia.

According to the researches of more recent times, among which should be mentioned especially those of Von Martens, Max Weber, and the Sarasins, it becomes evident that such a sharp boundary as Wallace drew does not exist. Not only is there none where he drew it, but no such line exists anywhere in the archipelago. Of course it is possible to draw a line which apparently bounds the distribution of some single group; and Pelseneer, upon the ground of the dispersal of molluscs, has constructed a new line which runs eastward of Celebes

and Timor, and which has been named by its author "Weber's Line." But taking the fauna as a whole it is quite certain that no line may be drawn; but, rather, we may lay out a transition zone in which the fauna of India and that of Australia are mingled, and wherein from the west to the east the Australian components increase more and more in number; and on the other hand, the Indian tend to die out. All of this region belongs to the eastern half of the archipelago from Celebes to New Guinea, and included in it we find a part of the Polynesian[2] Islands; but it is necessary to keep in mind that even the boundaries of this transition region are not sharply defined.

The justice of the position taken here will presently be sustained by some examples gleaned from among vertebrate animals, especially from fresh-water fishes, amphibians and mammals. All three groups, on account of the small likelihood of their being spread abroad over the sea, are of much importance to us.

First of all, however, the origin of the fauna of Australia merits a word. It is now commonly agreed that in past times this island formed an essential part of Asia, connected by a previously existing land-bridge which included the archipelago as it exists to-day. Formerly this connection was considered to have occurred during the Jurassic period (Neumayer's "Jura-Continent"). The finding, however, of deep sea deposits laid down in Jurassic times in different parts of the archipelago (*e. g.*, on Borneo, Celebes and Buru) has made it seem more probable that the mooted connection was delayed until the Cretaceous period; and along this connection, then, the marsupials and lung-fishes spread to Australia; as well as also the teleost, *Scleropages leichardti*, of which a near relative, *Scleropages* (= *Osteoglossum*) *formosus*, is now found upon Borneo and Sumatra, but upon no other

[2] Van Kampen uses the word *Polynesian* in a sense which is to us fundamentally wrong. He means to include the Melanesian Islands of the Bismarck and Solomon groups.

islands in the region lying between. It is not at all impossible that also a considerable portion of the present fauna of the Australian part of the Archipelago exists as a *Relictenfauna* coming down from the earliest times, although the geologic data warn us that Celebes and a considerable portion of the remaining archipelago was also covered by the sea during the Cretaceous period (Sarasin, 1901). So that, according to the latest geological evidence, it becomes apparent that in the Cretaceous period the archipelago could not all have been above water. Australia may well have received its ancient fauna from South America (Sarasin), or may equally well have had a connection with nearer India lying to the southward of the existing Archipelago (see Verbeek's *Molukkenverschlag*).

However that may have been, in any case the Indo-Australian continuity may well have been broken in Tertiary times, and thus the penetration of the Indian fauna into Australia have been brought to an end. Animals which up to that time had reached out into the archipelago would be unable any longer to reach Australia.

To such a class belong, for example, among the freshwater fishes, the family Cyprinidæ; among the amphibians, the Ranidæ; both of which are present in the Indian region by numerous representatives, while they are wanting in Australia. It is thus of importance for us to search out what may be the easterly boundary of such groups in the archipelago. Following Wallace's theory, the line which he constructed should answer this purpose. As a matter of fact the Cyprinidæ have served as one of the most important arguments for his opinion, since they did really stop at the supposed boundary line; since then, however, upon Bali we find a single pair of species of this family (*Barbus maculatus* and *Raspora argyrotænea*). During the expedition of the Siboga, Professor Weber, happened by chance to collect Rasbora upon Lombok (Weber, 1902, A); and I myself lately found the Gurami fish-ponds of the old pleasure-palace of Narmada filled with another

species of *Raspora*,[3] so that the boundary of the Cyprinidæ is thus moved to the eastward of Lombok.

Absolutely different is the real condition of the Ranidæ. This family has penetrated throughout all of New Guinea and western Polynesia; one single species, indeed (*Rana papua*), having reached the Cape York Peninsula of Queensland. Other Indian families of amphibians (Engystomatidæ, Pelobatidæ) have also reached to New Guinea. We see here then the boundaries of this transition region well defined, the westerly by the Cyprinidæ, the easterly by the Ranidæ.

Among the families of the strictly fresh-water fishes conditions are similar; and some have even reached

	Sumatra	Borneo	Java	Wallace's Line: Bali	Wallace's Line: Lombok	Timor	Celebes	Ambon	Halmahera	New Guinea	Australia
Fishes											
Notopteridæ	+	+	+	—	—	—	+	—	—	—	—
Osteoglossidæ	+	+	—	—	—	—	—	—	—	—	+
Cyprinidæ	+	+	+	+	+	—	—	—	—	—	—
Siluridæ	+	+	+	+	—	—	—	—	—	+	+
Symbranchidæ	+	+	+	—	—	—	+	—	—	—	—
Cyprinodontidæ	+	+	+	—	+	—	+	—	—	—	—
Melanotæniidæ	—	—	—	—	—	—	—	—	—	+	+
Ophiocephalidæ	+	+	+	—	—	—	+	+	+	—	—
Anabantidæ	+	+	+	+	+[4]	+	+	+	+	—	—
Nandidæ	+	+	+	—	—	—	—	—	—	—	—
Mastacembelidæ	+	+	+	—	—	—	—	—	—	—	—
Osphronomenidæ	+	+	+	+	—	—	—	—	—[5]	—	—
Amphibians											
Gymnophionians	+	+	+	—	—	—	—	—	—	—	—
Pelobatidæ	+	+	+	—	—	—	—	—	+	—	—
Hylidæ[6]	—	—	—	—	—	+	—	+	+	+	+
Bufonidæ	+	+	+	+	+	—	+	—	—	—	—
Engystomatidæ	+	+	+	—	+	—	+	+	+	+	—
Dyscophidæ	+	+	—	—	—	—	—	—	—	—	—
Ranidæ	+	+	+	+	+	+	+	+	+	+	+[7]

[3] It is entirely possible that these may have been brought in as eggs, along with the Gurami *Osphromenus olfax*, from Java.

[4] ***Anabas*, sp. found by me at Ampenan.**

[5] *Betta pugnax*, occurring upon Ternate according to Steindachner (1901).

[6] *Hyla dolichopsis*, recorded from Java by me (1907 A), undoubtedly introduced with plants brought into botanical gardens.

[7] **Confined to the Cape York Peninsula.**

farther than the Cyprinidæ. In these families one should include only those whereof all, or by far the greater majority, of the species are exclusively confined to fresh water. It is naturally evident that in other cases the possibility of their fortuitous transportation across the sea is not to be excluded. The appended table gives in outline the distribution of fresh-water fishes in the archipelago. It is gleaned, for the most part, from Weber (1894, 1897A), who has done more than any one else to add to our knowledge of the dispersal of the fresh-water fishes throughout the islands. For comparison a table is added giving the distribution also of the families of amphibians.

The eastern portion of the archipelago, including Celebes, possesses a very small fresh-water fish fauna. Those which are found most commonly in the rivers and lakes are, as Weber has pointed out, for the greater part "marine immigrants," that is to say, sea-fishes which have passed over to a fresh-water life. Of the true Indian fresh-water fishes which occur to the eastward of Wallace's line and Lombok are the Siluridæ; the New Guinea species, however, related to those of Australia and hence being in reality outside of our present range of discussion. The remaining ones are almost exclusively those which are able to withstand a drying-up—if this is not too long continued. These are, in truth, only a few species. *Haplochilus celebensis* among the Cyprinidontidæ does not get further than Celebes, nor does *Notopterus kapirat;* and two species of Symbranchidæ—*Symbranchus bengalensis* and *Monopterus javanensis*—*Ophiocephalus striatus, Anabas scandens* and *Anabas microcephalus* and possibly *Betta pugnax* are spread further to the eastward. The last-mentioned species have all a peculiar structure of the gill cavity which makes it possible for them to remain for a considerable time without water; and it has been shown by Volz for Monopterus that it may even live over through the dry monsoon without water.

The distribution of mammals in the eastern half of the Indian Archipelago is evidently not yet completely known. Even for New Guinea itself, with the exception of bats,

only a few species of mice and two of pigs (*Sus niger* and *S. papuensis*) have been discovered. Both of these last mentioned forms may perhaps have arisen from tame individuals which ran wild. Upon the Moluccas the only Indian mammals that occur are bats and mice, a single species of deer, perhaps also introduced; a few shrews, Viverridæ (*Viverra tangalunga* and *Paradoxurus hermaphroditus*), and wild pigs. Among the swine the well-known Babirusa is especially noteworthy, which is found only upon Celebes and Buru. The Moluccas (Batjan) have a single ape (*Cynopithecus niger*) in common with Celebes. But even here again it has frequently been suggested that this form was probably also introduced. In comparison with the richness in mammals of the Greater Sunda Islands, Celebes falls in with the Moluccas as showing their paucity.

The eastern half of the archipelago, in accordance with its character as a transition region, is not alone habited by immigrants which have come in from the west, but has received its fauna in part from Australia. If we take the three classes of animals which we have mentioned before, we then find here also a strong element which has spread itself even further from its origin, in this case Australia. Upon New Guinea the Melanotæniidæ among the fishes, the Hylidæ among the amphibians, and the marsupials and Monotremes among the mammals are well represented. These fishes have not dispersed themselves very far (the Melanotæniidæ not being known to have reached beyond the Aru Islands). The amphibians themselves are also almost as narrowly confined to the nearby islands, and have not even got as far westward as Celebes. The marsupials have got as far as Celebes and Timor. Although fifty-one species have been made known from New Guinea itself, so that only a small portion of these have gone farther westward; of these two have got to Celebes, both of the species belonging to the genus *Phalanger*. The fauna of New Guinea has, when one considers the Indian elements in it, about as much derived from the fauna of

Australia as that of Sumatra, Borneo and Java has derived from the mainland of Asia.

A general survey of all conditions leads to the conclusion that in post-Cretacean times there was a broad connection between the three Greater Sunda Islands and Asia on the one hand, and between New Guinea and Australia upon the other; that further also between the Sunda Islands and New Guinea a connection must have existed which was really less easy to pass over. The configuration of the bottom of the ocean supports this opinion. The western half of the archipelago is united with Asia, standing on a plateau of not more than fifty fathoms depth; New Guinea is separated from Australia by a similarly shallow sea. An elevation of the sea bottom of 45 meters would connect the Greater Sunda Islands with the mainland of Asia; while on the other hand a rise of 20 meters is all that is necessary to bring about the joining of New Guinea with Australia. The seas intervening between these two regions have, on the contrary, for the most part a great depth.

There still remains much to do in substantiation of the proof of these conclusions; and the islands and island groups of the archipelago are still a fruitful field of inquiry for those who may be interested.

As already remarked above, Sumatra, Java and Borneo lie upon a shallow submarine plateau which binds them to further India. Upon this same plateau lie also a host of lesser islands such as Banca and Billeton, Madura and Bali. All of these islands, as well as those which lie along the west coast of Sumatra, and which are surrounded by a sea of considerably greater depth, possess a fauna which in all its principal characteristics is essentially that of the Malay Peninsula. Here alone one finds the great Indian mammals, such as the Orang Utan, the tiger, the leopard, the Malayan bear, elephant, tapir, rhinoceros and bantang. Even still more evident is the relationship of the mainland when one takes into account the finds among the fossils. Dubois has uncovered a Tertiary fauna upon Java that bears the most marked resemblance to the Pliocene Siwalik

fauna of Hindustan. Here he found, for instance, remains of Hippopotamus, Stegodon, a species of antelope, Hyæna, Gavialis, etc.

Taking the present condition alone into account, Sumatra and Borneo more than the others have a fauna that is almost identical with the fauna of the Malay Peninsula. Java shows a greater difference; whereupon one may draw the conclusion that it broke off earlier than the other islands from the mainland, since between Java and Sumatra there was more migration than between Java and Borneo, so that it was separated earlier from the last mentioned island than from Sumatra. The Javan Sea, as the Sarasins have determined from a study of the land snails, is of very ancient date.

On the other hand, Java has some mammals, *Rhinoceros sundaicus*, *Trajulus stanleyanus*, *Viverricula malaccensis*, *Helictus orientalis*, in common with the mainland, which up to the present have not been found upon either Sumatra or Borneo. So far, for this state of affairs absolutely no satisfactory explanation has been found.

We might also say of Borneo that it has received a small portion of its fauna evidently by way of Palawan and the Sulu Archipelago from the Philippines, and so directly from south China, and indeed from the Himalayan region itself.

Celebes has always been the great bone of contention from a zoogeographic point of view. We have already seen that Sal. Müller and originally Wallace considered it as belonging to the Australian half of the archipelago. Now, especially through the labors of Max Weber and the Sarasins, it has been made evident that its fauna is essentially Indian, even though it may be mixed with a few Australian types.

But even so, the fauna of Celebes is as yet only partly elucidated. We find here an astonishing number of peculiar types which no one has been able to find upon the other larger islands of the archipelago; and so there must always be a question as to the origin of its fauna.

The first peculiarity is the occurrence of a number of

animals which find their nearest relatives not in the further Indian Archipelago, nor yet even upon the continent of Asia, but in Africa itself. Taking the number of these species of animals together, we must conclude that they are of very ancient origin indeed. Among the birds which must be grouped in this way are such species as *Coracias temmincki* and *Cittura*, the most primitive kingfisher; among the mammals two species of monkey, namely *Macacus maurus*, and its next of kin, *M. arctoides*, which belongs in Hindustan, and *Cynopithecus niger*, most closely related to the African baboons;[8] in addition, the strange *Babirusa*, a pig that is more like the African warthogs than any other variety of swine. The dwarf-buffalo, or Anoa (*Bos depressicornis*) may also be considered as a relic-species, of which its only near living relative, *Bos mindorensis*, inhabits the Philippines.

The explanation of this relic-fauna the Sarasins take to be an old invasion evidently spread out from Java, which most likely happened in the Miocene period. It can not have taken place earlier, since the same investigators were astonished at the geologic evidences that Celebes in Eocene times was wholly covered by the sea. The more recent fauna (that which shows itself among mammals in the abundance of species of squirrels) arrived later, and in all probability entered Celebes along the same land connection. This explanation is not entirely satisfying, since it does not make evident why these animals that we have mentioned exist on Celebes, but have died out everywhere else. On the other hand, that such things really can occur is proved by the abundance of the finds of fossil remains of animals in places where they no longer exist. The epoch-making discoveries of Dubois are of weighty import in this connection.

A further peculiarity of the fauna of Celebes is its great difference from that of Borneo. The Sarasins

[8] Matschie brings the monkeys of Celebes together into one genus (*Papio*), while he differentiates a number of new local races upon the same island. Trouessart, in the supplementary part of his "Catalogus mammalium," has united all these forms as varieties of one single species.

have announced that both islands have not one single species of animal common to them which is not also found upon Java, Sumatra or the Philippine Islands. There is not the slightest possibility of there having been a direct land bridge between Celebes and Borneo across the Straits of Macassar since the very earliest geologic times. This difference between Celebes and Borneo is beyond doubt one of the real reasons for the unjustifiable opinion of Wallace and for the placing, as he did, of his boundary line.

That the Java sea is, according to the Sarasins, of great age is shown by the fact that a curved line may be drawn through this sea and continued into the Straits of Macassar, which terminating blindly, so to speak, at both ends, cuts the archipelago into two portions, or, we might better say, bounds one part where the islands of younger geologic age have apparently had no connection with the mainland. It has thus an entirely different significance from the boundary line as it was formerly drawn.

A third peculiarity of Celebes upon which Weber has laid particular stress is the paucity of certain groups of animals in comparison with the three Greater Sunda Islands. Weber has considered the fauna of Celebes as being essentially an impoverished Indian one. This poverty appears best brought out by the appended table,[9] wherein the comparison as regards the approximate extent of the islands is given.

	Sumatra	Borneo	Java	Celebes
Surface in sq. km	431,000	733,000	126,000	179,000
True fresh-water fishes[10]	212	202	131	4
Amphibians	50	78	37	25
Reptiles	175	191	129	87
Mammals (exclusive of bats)	115	133	68	39

[9] These data in this table are drawn for the most part from Weber (1894), Popta (1905–6), and Volz (1907), for the fishes; Van Kampen (1907 B), for the amphibians; Sarasin (1901) for the reptiles; Tjeenk Willink (1906) and Schneider (1905), for the mammals.

[10] These are drawn from the same families that were mentioned in the table upon page 547.

This difference is noticeable among the fishes above all others. On the other hand, the difference is less among the birds, and the opposite holds for land and fresh-water molluscs whose number is reckoned by the Sarasins for Sumatra as 129 species; Borneo, 311; Java, 233, and Celebes, 238.

Weber explains the poverty of fauna in this manner: that Celebes, as we understand it to-day, has not long been in its present condition, but rather that it was formed by the uniting of a number of small islands which, as is always the rule in such cases (especially among the fresh-water fishes) possess a sparse or poor fauna. In this same wise is it made evident why the fresh-water mussels (Unionidæ) which occur upon the continent of Asia and Australia, and upon the Greater Sunda Islands, are lacking on Celebes. Von Martens comes to this same conclusion, that they (along with other generally distributed families of fresh-water molluscs) do not occur upon small islands. They are wanting thus upon the Moluccas and on Celebes, where the entire fauna has been made up by the merging together of those of several smaller islands to form a single one.

The opinion of the Sarasins is somewhat different from the explanation of Weber. They are of the opinion, brought forward as especially important, that between the different parts of the island ancient faunistic differences are demonstrable, a peculiarity of the fauna of Celebes which has been thoroughly investigated by them. The Sarasins have taken this up especially from the point of view of distribution of land and fresh-water molluscs. Von Martens had already noticed that north and south Celebes possessed hardly a single species of mollusc in common; and the Sarasins made evident that there existed an easterly mollusc fauna, besides a well-differentiated fauna in the great lakes of central Celebes. Other animals exist, divided from each other in this same manner. So among the mammals, the Babirusa and the crested baboon, *Cynopithecus*, are found in the northern

portion of Celebes only; as is also that remarkable bird *Megapodius cumingi*, as well as some others.

Another point emphasized is the fact that the molluscs of the different peninsulas of Celebes show closest relationship with the island lying near them. The Sarasins found among the groups of animals which they studied that the species which have survived and which have become peculiar now to Celebes, as well as those which have a wider spread at the present time through the archipelago, show in part a relationship to species from Java, in part to those from the Philippines, or from the Moluccas, or again from the Lesser Sunda Islands, especially Flores. The proportion of these four components of the fauna of Celebes is about the relationship of 4:3:2:1. Here again is emphasized the overwhelmingly Indian characters of Celebes, since alone among these last two mentioned smaller groups no Australian species have been found. A close relationship with Borneo is, as we have mentioned previously, entirely non-existent.

The explanation of the Sarasins is this. Celebes rose from the sea in Eocene times, and in Pliocene times especially received its fauna along four land bridges, each of which connected the island with one of the previously mentioned islands or island groups. The position of these bridges is still traceable through submarine shallows, or else by groups or chains of islets. The Java bridge ran from the southern peninsula out through what are now Postillon, Paternoster and Kangean Islands, to eastern Java. The Philippine bridge bound the northern peninsula with Mindanao, and included the present Sangi and Talaut groups. The Moluccan bridge went off from the eastern peninsula; and united together the Peling and Sula Islands, and apparently then split up into two bridges, one of which ran off to the Obi and Halmahera groups, the other to Buru. This last connection is postulated by the geographic distribution of the Babirusa, and also by the birds. The latter, from the mountains of Buru, show a close relationship with Celebes. However, during the expedition of the Siboga,

the strait between Buru and the Sula Archipelago was found to be of considerable depth (about 4,100 meters), an argument against any such land connection.

It occurs to me that the past events which have been reconstructed by the Sarasins are just as well explained by Weber's opinion, which is that the separated islands, which gave rise to Celebes, by consolidation, have received their fauna in the way which the Sarasins have suggested. The point of difference is indeed simply a question of interpreting the significance of the earlier history. In either case it is entirely plausible that Celebes has received its fauna from the south,[11] the north, and the east; not directly from Borneo, but rather by means of small islands or narrow land bridges; which fact has had a great influence on the impoverishment of the fauna. On the other hand, animals from Celebes have been enabled to spread out along these same land connections, so that occasionally we find evidences among the Philippines and the Lesser Sunda Islands of this having happened by their having certain common animal types.

It is peculiar that the truly Indian character of Celebes (the great westerly island of the transition region) remained unsuspected for so long; while on the other hand, no one doubted, but rather laid stress upon, the Australian relationship of that vast easterly island, New Guinea, the fauna of which is fully as Indian as that of Celebes is Australian. It simply happened that those groups of animals which at once were most evident, and which had been most frequently used in elucidating zoogeographical questions—especially birds and mammals—are preponderatingly Australian upon New Guinea, and happen to show upon Celebes also a considerable Australian admixture. Had earlier investiga-

[11] Weber brings into existence two different land bridges as an argument to explain the difference between the fauna of Java and Flores. He is inclined to the opinion that there was here a land mass of considerable extent which has given rise to the great depths of the Flores Sea by an extensive sinking.

tors laid more stress upon the amphibians, then an entirely different result would have been arrived at: New Guinea possesses here again 39 species which belong to Indian families as against 24 Australian.[12] Among other groups of animals New Guinea is more Indian than Australian. This is the case with the scorpions and the earthworms.

New Guinea, then, has a mixed fauna, whereof the Australian elements are explained by the existence of a now broken connection with Australia; and whereof the Indian elements evidently arrived from the Moluccas. The Sarasins have constructed, in explanation of this, two bridges, one of which connected New Guinea with Halmahera—the New Guinea bridge of Kuckenthal (1903); the other, with Ceram. The Aru and Ke islands range themselves along with New Guinea. Upon both, for instance, we find a true kangaroo, *Macropus brunii* [*sic*], an animal which does not occur further to the west of New Guinea. The Aru Islands possess a fresh-water fish of the family Melanotæniidæ, the remaining members of which are confined to Australia and New Guinea (Weber, 1907B). This same relationship is shown by birds such as crown-pigeons, birds of Paradise, and cassowaries, as well as among amphibians and other groups. One can, therefore, take it for granted that at the same time as New Guinea both of these two island groups were united with Australia, although the Ke Islands are cut off by a greater depth of sea.

From the already mentioned faunistic difference between Celebes and New Guinea, it follows that for many families and genera of animals both the westerly as well as the easterly boundaries must lie in the Moluccas. Here one would expect to be able to place a boundary line which would exactly fit each special case. But here we are hindered further by the fact that just these is-

[12] In this are included the species described by me in a memoir the preliminary of which will appear in Nova Guinea. See also Van Kampen (1906). [The paper in "Nova Guinea" has already been published.—**Translator.**]

lands are the ones which are still only incompletely known. With the exception perhaps of certain groups of animals—birds, butterflies, etc.—which on account of their value are specially sought for, there are great gaps in our knowledge. Only during the last few years have Halmahera, Ternate and Batjan been systematically studied by Kuckenthal. These islands then are the best known. Obi, Buru, Ceram, the Sula Archipelago and others are no more than zoologic blanks upon the map. It is a fact that upon the Sula Islands a short time ago 19 species of land snails were collected, while only a short time before only one single species was known (Schepman). These last-mentioned islands are of importance as having belonged to the Molucca bridge of the Sarasins.

Another question is whether the Moluccas have received their Indian fauna along this Molucca bridge from Celebes, as the Sarasins claim, or along still a different way, as perhaps through the Talaut Islands from the Philippines, as some cases tend to show.

These questions must wait for a definite answer until researches have brought more light to bear upon them. Before this we can only go so far as to say with certainty that the fauna of the Moluccas is a mixed one, as is that of New Guinea; and that in large part on account of the generally small size of the islands both the Indian and Australian components are found impoverished in comparison with the neighboring greater islands.

Hardly more complete is our knowledge of the Lesser Sunda Islands. Weber (1902) placed them among the very least known of any in the archipelago. Here remain a number of knotty questions still to be explained, although it has been definitely proved that the sharp line which Wallace drew between Bali and Lombok must be given up for good and all. The existence of one of the most fundamental supports of this boundary was disproved by the expedition of the Siboga; and that was regarding the great depth of the Lombok Straits. Indeed, this strait is somewhat deeper than that between the other

islands of the series from Bali to Ombaai; and the Sarasins believe that it was in reality one of the oldest, although more recent than the Strait of Macassar, and thus well within the Secondary Epoch. This allows us to explain a certain faunistic differentiation between Bali and the other islands; for we know, for instance, that cockatoos do not occur further to the westward than Lombok. This was one of the weightiest arguments which Wallace used. However, cockatoos live in the Philippines, and thus well to the westward of his own line. Weber points out that the fauna of the Lesser Sunda Islands is in large part an impoverished Indian one derived from Java, beside which there occurs a small element from Celebes (along the Flores bridge). So also by the same means has come a slight infiltration of Philippine forms. Here also we find a few Papuasian or Australian species. Timor appears, indeed, to have received some animals directly from New Guinea or Australia (birds, *Hyla*).

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SHORTER ARTICLES AND DISCUSSION

BIOMETRIC ARGUMENTS REGARDING THE GENOTYPE CONCEPT[1]

Some . . . persons vainly seek by dialectics and far-fetched arguments, either to upset or establish things that are only to be founded on anatomical demonstration, and believed on the evidence of the senses. He who truly desires to be informed of the question in hand, and whether the facts alleged be sensible, visible, or not, must be held bound either to look for himself or to take on trust the conclusions to which they have come who have looked; and indeed there is no higher method of attaining to assurance and certainty.—William Harvey, *Second Disquisition to John Riolan, Jun.*

In a recent number of this Journal[2] Dr. J. Arthur Harris has published a general attack on the pure-line or genotype concept of inheritance. In the course of this paper its author sees fit to criticize certain work done by the present writer and his former colleague, Dr. Frank M. Surface. These criticisms in the main seem to me, upon analysis, to rest on either a misconception of what our results actually are, or else a lack of understanding of the real facts regarding certain of the biological points involved. If this is the correct view, it means that our presentation of pertinent data has been either obscure or incomplete or both. It is the purpose of this note to endeavor, if possible, to remedy this defect in some degree at least.

The points made by Harris in criticism of the work done in this laboratory may be considered *seriatim*.

1. In a section entitled "Characters which are not Inherited at all can not be Taken to Prove that Selection in General is Ineffective," Harris very cautiously avoids the direct statement that fecundity in fowls is not inherited, but since about one half of the section (pp. 353–356) is devoted to a discussion of the work of the Maine Station on this matter, it is not unfair to suppose that he is of opinion that this work illustrates and exemplifies the dictum which stands as the title of the section. He concludes in a later section that the present writer's investiga-

[1] Papers from the Biological Laboratory of the Maine Experiment Station, No. 28.

[2] Amer. Nat., June, 1911.

tions indicate "that the high-laying mothers tend to produce low-laying daughters; selection to increase egg production actually decreases it."

Definite numerical data tending to show that fecundity in the domestic fowl *is* inherited has been presented by the writer in the June, 1911, number of the AMERICAN NATURALIST (pp. 321–345). It obviously need not be repeated here. Any interested person may examine the data and draw his own conclusions as to whether "selection to increase egg production actually decreases it," when this selection takes the form of isolating genotypes of high fecundity.

2. The second point made by Harris is against what was intended to be a popular bulletin on sweet corn[3] in the introduction to which the following statement was made: "It is the purpose of this bulletin to give a brief account of the general features of the experiments carried on during the past three years in sweet-corn breeding. Further discussion of the technically scientific results of this work is reserved for later publication." No such publication has appeared.

The criticism of this bulletin is included in a section headed "Improvement for any Single Character can not be Supposed to be Unlimited." The facts are these: In 1907 selection was begun for earliness in an excellent strain of sweet corn. A *marked* gain was made in the quality after one year's selection. No further gain has been made though selection has been continued.

It is Harris's contention that probably after one year's selection the strain had reached its physiological limit in earliness, and that the result obtained can not be urged against the biometric theory respecting selection, nor in favor of the genotype concept. He further gives the reader the impression that Dr. Surface and I regarded these results on earliness as having an important and critical bearing upon theories of selection and inheritance. For the benefit of those readers who do not follow agricultural literature it may be well to quote the final conclusion (numbered 14) printed on p. 307 of the bulletin Harris criticizes:

> No attempt is made at present to discuss the biological basis of the improvement in earliness observed to follow selection for that character in these experiments. *We are inclined to the belief that much, if*

[3] Me. Agr. Expt. Station, Bulletin 183.

not all, of this improvement is in reality a physiological rather than a genetic or hereditary phenomenon.[4] The whole subject of breeding for earliness is one which needs more critical discussion and experimentation than has hitherto been given it.

The same opinion is expressed in the body of the bulletin (p. 302). How one could take a more emphatically agnostic position than this regarding the interpretation of the results of the selection of maize for earliness is not evident.

In regard to characters other than earliness, such as ear conformation, fineness of grain, yield, etc., which Harris does not mention in his critical remarks, it was and is our conclusion that the results in hand indicated that these characters were not inherited in accordance with the so-called "law of ancestral inheritance," but that our results with these characters gave support, so far as they went, to the genotype concept, thus agreeing with the findings of other students of maize. Whether from too hasty reading of the bulletin criticized or some other reason, Harris has made it appear in his paper that we had earliness in mind in drawing this conclusion. I trust that our position is now clear.

Harris assures us (p. 359) that he has "no malicious desire to differ" from us. This it is a pleasure to know for two reasons: one is that a person would dislike to think that he was the butt of malicious and persistent personal attack from a scientific worker: the other is that since there is no intention on his part to be personal and since ours is the *only* work on maize with which he finds fault or feels it even necessary to mention, it must mean that he finds nothing to object to in the only critical, analytical evidence on genotypes in maize which, so far as the writer is aware, has ever been published, namely, that of East and Shull. It is a distinct gain thus to find that there is one body of evidence in favor of the genotype concept which its critics unreservedly accept.

3. It is suggested by Harris that 200 eggs per year represents about the attainable limit of egg production in fowls, and that the reason no improvement was made in our selection experiment was that this physiological maximum had been reached. Here two points need to be made plain. The first is that 200 eggs per year is *not* the physiological maximum of egg production in the domestic fowl. As evidence here the case of a pullet

[4] Not italicized in original.

which laid over 300 eggs in a year may be cited. While the case did not occur in the poultry yards of this station, there is no doubt as to its correctness. Furthermore, the case is by no means an isolated one, similar records having been obtained under controlled conditions in other parts of the world. This record was made by a cross-bred Orpington pullet in New Jersey. The history of her laying is as follows: She began laying on November 20, 1909. Up to August 25, 1910, she laid practically continuously, producing in that period 275 eggs. She then went broody, and in late September and October moulted. The September record was 13 eggs; the October record 12 eggs, and up to November 9, 6 eggs, making a total production of 306 eggs in 11 days less than a full year.

Further evidence of the same sort is furnished by the report of the last Queensland (Australia) laying competition which has just come to hand.[5] In this competition 150 pullets took part, comprised in 25 pens of 6 birds each. The aggregate egg production of 12 months, from April 1, 1910, to March 31, 1911 (the natural "laying year" in the southern hemisphere), was 31,165, or an average per bird, taking the *whole lot together*, of 207.77 eggs. The three highest pens (of 6 birds each) made average records per bird of 253.33 eggs, 238.83 eggs and 218.67 eggs, respectively.

The second point is that the Maine Station *flock* never attained an *average* production of 200 eggs per bird, or anything like it. But it can not be supposed that a *physiological limit of selection* for production is reached until the *mean* egg production per bird for the *flock* has reached about the physiological limit of the *individual*. The point apparently not clearly grasped by Harris is this: for a long period of years prior to 1898 when the mass selection experiment at the Maine Station was begun, the strain of birds with which it was begun had been under the observation of the man who inaugurated the experiment, the late Professor Gowell. The mean annual production of this flock had been, according to his statement, which there is no reason to doubt, about 125 to 135 eggs per bird. Now there were then known and are now known many flocks of birds which produce an average of 150 to 160 eggs per bird per annum. To attempt to raise the average production of the Maine Station *flock* from say 130 to say 150 eggs per bird per annum by mass

[5] *Feathered Life*, Vol. 12, p. 450, 1911.

selection could hardly by any stretch of the imagination be considered to be approaching the physiological limit of fecundity of the fowl. This is precisely what was attempted during a period of eight years, and was not accomplished. While there is no doubt in all organisms a physiological limit beyond which selection of any kind can not carry the strain or race, such a limit was most certainly never even remotely approached in the course of the mass selection experiment at the Maine Station.

4. Harris emphasizes by the use of italics the fact that the only correlation coefficients between mother and daughter in respect to egg production which I have ever published, while sensibly equal to zero having regard to the probable errors (with a single exception where daughter averages are used), yet deviated in the *negative* direction[6] when they departed from zero at all. Lest some one should attach some importance to this circumstance it may be said that these coefficients to which he refers cover only one year's work (1907–08). Since that time I have calculated the coefficients of correlation in respect to fecundity between mother and daughter and grandmother and granddaughter for the years 1908–09 and 1909–10, for various age classes of mothers, etc. These correlations involve over 1,000 daughters and over 200 mothers. *All of these correlations are sensibly zero*, having regard to their probable errors. Of 11 such coefficients 8 deviate from zero on the positive side and 3 on the negative side. Putting the 1907–08 published coefficients with these it gives, out of 16 coefficients, 10 deviating from zero in the plus direction and 6 in the minus direction. Certainly it is difficult to see how this could be made to indicate that "high-laying mothers tend to produce low-laying daughters."

By way of conclusion it may be said that the writer hopes that what is here set forth will make clear the facts regarding the points criticized by Dr. Harris in the work from the biological laboratory of the Maine Station. So far as concerns his argumentation respecting the genotype concept as a whole, or his personal opinion of the critical value of the work done in this laboratory no discussion will be entered upon by the present writer. Since the merits of both cases rest upon nothing

[6] Harris implies that this was true of *all* 1907–08 correlations. This is not so, as any one may see by turning to p. 71 of Bulletin 166, where of the five coefficients published, and these are *all* which have been published up to the present time, three are negative and two are positive.

but an accumulation of plain, unadorned facts available to any one's inspection, it seems useless to try to bolster either of them up by the dialectic methods of a lawyer's appeal to the jury.

RAYMOND PEARL.

June 21, 1911.

ON THE FORMATION OF CORRELATION AND CONTINGENCY TABLES WHEN THE NUMBER OF COMBINATIONS IS LARGE

IN earlier numbers of this JOURNAL two papers on that useful tool, the correlation coefficient, have appeared. The first[1] explains and illustrates a convenient method of carrying out the arithmetical routine of calculation, while the second, by Professor Jennings,[2] describes a method for obtaining the coefficient for symmetrical tables without the labor of actually rendering the tables themselves symmetrical.

The purpose of this note is to point out a method of preparing correlation tables where the number of combinations is large. Such tables are not infrequently needed. Suppose, for

[1] Harris, J. Arthur, "The Arithmetic of the Product Moment Method of Calculating the Coefficient of Correlation," AMER. NAT., Vol. 44, pp. 693–699, 1910.

In a note on this method of calculating the coefficient of correlation, Professor Jennings (AMER. NAT., Vol. 45, p. 413, 1911) suggests reduction in size of the moments by designating the lowest grade by 0 and the succeeding ones by 1, 2, 3, ... n. In this he is quite justified. I have frequently used the scheme he suggests during the last several years, but I did not refer to it particularly in my note, and for two reasons. First, I thought the point sufficiently covered by the statement that the rough moments may be taken about any arbitrary point as origin, and by the suggestion that when the range is very great it may pay to use the conventional methods in calculating the standard deviations. Second, according to my experience it is better, whenever possible, to keep the actual values. When one uses a mechanical calculator the arithmetical routine is (after a little practise) not out of proportion to the advantages. Under many circumstances these are very great: (a) all the values have a direct biological (physical) significance, (b) the means of arrays may at once be obtained for testing linearity of regression, (c) tables for different lots of material may be combined or separated at will by merely summing or segregating their moments, and finally (d) I shall show in a forthcoming paper how these moments, once calculated, may be of much service in obtaining some of the more difficult correlations.

[2] Jennings, H. S., "Computing Correlation in Cases where Symmetrical Tables are Commonly Used," AMER. NAT., Vol. 45, pp. 123–128, 1910.

instance, that one wishes to correlate between the hatching quality of the eggs of sisters in the domestic fowl, as Pearl and Surface[3] have actually done. If each family be composed of only ten pullets and there be only fifty families the number of entries in the symmetrical correlation table will be $10 \times 9 \times 50 = 4{,}500$. Or again, if one be interested in determining whether the dimensions or proportions of the blood corpuscles differ from individual to individual in an animal, say the tadpole,[4] and have measurements of twenty-five corpuscles in each of 100 individuals, he may have to form a correlation table of 60,000 entries. Much larger tables than this have been formed. The labor is of course excessive, and this has been one of the factors limiting their application to problems of morphology, physiology and heredity.

In many cases the routine, as I have found from considerable experience, can be profitably carried out as follows.

The individuals of each class are seriated separately and the frequencies entered in horizontal rows in a table of vertical columns, each devoted to one of the grades of variates, g_{m+1}, g_{m+2}, . . . g_{m+n}. A second table, exactly like the first in width of column and row is prepared and cut into strips by columns. Each of these columns is moved successively across the surface of the original table, and the frequencies which are in juxtaposition are multiplied together and their products summed and entered on a correlation blank, in the compartment corresponding to the captions of the two columns. This is repeated for all the columns *except the one identical with the strip.* If the strip be for grade g_{m+2}, the multiplications and summations from once passing it over the original table give the whole relative array associated with it as subject, except the frequencies of the diagonal cell, $g_{m+2} - g_{m+2}$.[5] To obtain these each frequency on a strip is multiplied by itself less one and the products summed.

It is not absolutely necessary, since the table is symmetrical,

[3] Pearl, R., and Surface, F. M., "Data on Certain Factors Influencing the Fertility and Hatching of Eggs," Bull. Me. Ag. Exp. Sta., No. 168, pp. 147–151, 1909.

[4] For actual cases, see K. Pearson, "A Biometric Study of the Red Blood Corpuscles of the Common Tadpole (*Rana temporaria*) from the Measurements of Ernest Warren," *Biometrika*, Vol. 6, pp. 402–419, 1909.

[5] Diagonal cell is the term applied to a compartment of a row extending diagonally across the correlation surface. In symmetrical tables they contain the frequencies for identical values of the subject and relative.

to obtain the products of the frequencies of all of the columns by all the strips, but by doing so a check is obtained for all entries except those of the diagonal cell.

The great advantage of this method is that it replaces mental and pencil drudgery with rapid mechanical calculation. Clipping the movable column by the side of the one with which it is to be compared in the table, one can obtain the products and the sum of the products simultaneously on a Brunsviga,[6] by merely multiplying the successive pairs of frequencies together and allowing the products to accumulate. Of course the frequencies for the diagonal cell can be quickly obtained, by summing the $n(n-1)$ values for the individual column, in precisely the same manner.

Purely as an illustration of method the intra-individual or homotypic correlation for number of seeds developing per pod in a series of Broom plants (*Cytisus scoparius*)[7] collected at Woods Hole in the late summer of 1907 will now be determined.

TABLE I

SEEDS PER POD FOR TWENTY-THREE INDIVIDUAL PLANTS

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
1	–	–	2	2	1	9	7	10	9	15	9	11	4	3	8	3	3	3	1	–	–	100
2	–	+	—	—	—	—	1	3	3	6	12	6	14	13	12	5	5	11	5	3	1	100
3	–	–	—	—	1	—	2	4	2	4	10	11	7	14	11	12	13	7	2	–	–	100
4	–	–	—	—	—	5	3	7	12	15	14	16	16	7	3	2	—	—	—	–	–	100
5	–	1	—	1	1	4	5	8	10	10	13	12	10	18	4	2	1	—	—	–	–	100
6	–	–	7	7	7	12	8	11	8	8	7	9	7	7	2	—	—	—	—	–	–	100
7	–	–	—	1	1	7	2	5	5	10	7	16	7	9	10	9	2	8	1	–	–	100
8	1	1	2	1	4	3	4	9	8	8	16	9	9	14	7	4	—	—	—	–	–	100
9	1	–	—	—	1	7	9	4	7	11	18	12	10	7	4	6	3	—	—	–	–	100
10	–	–	2	1	3	5	8	9	7	6	14	11	12	10	6	5	1	—	—	–	–	100
11	–	1	2	2	4	3	8	8	8	8	10	13	11	6	5	5	3	3	—	–	–	100
12	–	–	2	1	6	10	17	17	15	10	11	4	6	1	—	—	—	—	—	–	–	100
13	–	–	—	1	—	1	2	3	12	14	12	14	10	12	12	3	3	1	—	–	–	100
14	–	–	—	1	5	5	9	6	11	11	9	9	11	6	9	5	2	1	—	–	–	100
15	–	–	—	—	—	5	3	6	5	4	8	10	8	8	13	13	9	5	3	–	–	100
16	–	–	1	—	1	7	6	7	7	7	9	8	8	8	8	9	8	4	2	–	–	100
17	–	–	—	1	1	8	9	10	7	11	10	14	13	12	3	1	—	—	—	–	–	100
18	–	–	—	—	—	2	1	3	6	12	15	13	13	7	15	8	4	1	—	–	–	100
19	–	–	—	—	1	5	5	7	15	12	11	14	13	11	4	2	—	—	—	–	–	100
20	–	–	—	3	4	6	10	12	6	6	12	10	11	6	6	3	3	2	—	–	–	100
21	–	–	2	2	1	1	4	4	8	5	11	13	10	9	7	3	3	1	—	–	–	84
22	–	1	2	5	5	13	8	8	6	13	5	6	6	2	—	—	—	—	—	–	–	80
23	–	–	2	14	12	11	11	9	6	7	1	1	—	—	—	1	—	—	—	–	–	75
	2	4	24	43	59	129	142	170	183	213	244	242	216	190	149	101	63	47	14	3	1	2,239

[6] A Comptometer will also do.

[7] The variability of these has already been compared with that of Pearson's English series. See "Variation in the Number of Seeds per Pod in the Broom, *Cytisus scoparius*," AMER. NAT., Vol. 43, pp. 350–355, 1909.

TABLE II

INTRA-INDIVIDUAL OR HOMOTYPIC CORRELATION FOR SEEDS PER POD IN THE BROOM

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
0		1	2	1	5	10	13	13	15	19	34	21	19	21	11	10	3					198
1	1		6	9	14	23	25	33	32	39	44	40	36	40	16	11	4	3				376
2	2	6	58	105	122	201	196	232	197	207	212	207	173	147	88	51	28	18	4			2,254
3	1	9	105	256	287	390	374	390	313	373	276	300	240	195	123	74	36	30	3			3,775
4	5	14	122	287	286	477	536	559	482	511	489	446	412	320	208	147	70	48	6			5,425
5	10	23	201	390	477	898	1,009	1,130	1,066	1,268	1,204	1,227	1,049	824	586	424	223	166	45			12,220
6	13	25	196	374	536	1,009	1,066	1,284	1,230	1,324	1,435	1,328	1,220	943	649	458	265	161	39	3	1	13,559
7	13	33	232	390	559	1,130	1,284	1,338	1,446	1,581	1,749	1,677	1,513	1,267	885	598	351	253	70	9	3	16,381
8	15	32	197	313	482	1,066	1,230	1,446	1,516	1,835	1,990	1,965	1,762	1,470	1,065	656	365	240	62	9	3	17,719
9	19	39	207	373	511	1,268	1,324	1,581	1,835	2,008	2,296	2,330	2,038	1,694	1,320	814	457	345	89	18	6	20,572
10	34	44	212	276	489	1,204	1,435	1,749	1,990	2,296	2,648	2,708	2,489	2,189	1,671	1,104	669	462	138	36	12	23,855
11	21	40	207	300	446	1,227	1,328	1,677	1,965	2,330	2,708	2,612	2,448	2,170	1,684	1,128	671	494	125	18	6	23,605
12	19	36	173	240	412	1,049	1,220	1,513	1,762	2,038	2,489	2,448	2,094	1,956	1,488	959	575	442	135	42	14	21,104
13	21	40	147	195	320	824	943	1,267	1,470	1,694	2,189	2,170	1,956	1,812	1,397	928	598	458	145	39	13	18,626
14	11	16	88	123	208	586	649	885	1,065	1,320	1,671	1,684	1,488	1,397	1,228	919	618	480	155	36	12	14,639
15	10	11	51	74	147	424	458	598	656	814	1,104	1,128	959	928	919	640	506	361	118	15	5	9,926
16	3	4	28	36	70	223	265	351	365	457	669	671	575	598	618	506	356	275	99	15	5	6,189
17		3	18	30	48	166	161	253	240	345	462	494	442	458	480	361	275	254	103	33	11	4,637
18			4	3	6	45	39	70	62	89	138	125	135	145	155	118	99	103	30	15	5	1,386
19							3	9	9	18	36	18	42	39	36	15	15	33	15	6	3	297
20							1	3	3	6	12	6	14	13	12	5	5	11	5	3		99
	198	376	2,254	3,775	5,425	12,220	13,559	16,381	17,719	20,572	23,855	23,605	21,104	18,626	14,639	9,926	6,189	4,637	1,386	297	99	216,842

The original data appear seriated by individual plants in Table I. From this we derive the symmetrical intra-individual correlation surface, Table II.

Working by the conventional product moment method, but taking all moments around 0 as suggested elsewhere in these pages,[8] we get:

$$\Sigma(x') = 2{,}179{,}781, \qquad \nu_1' = 10.0524 = A,$$
$$\Sigma(x'^2) = 24{,}578{,}235, \qquad \nu_2' = 113.346284,$$
$$\Sigma(x'y') = 22{,}438{,}814, \qquad \mu_2 = 12.295679 = \sigma^2,$$
$$N = 216{,}842. \qquad \Sigma(x'y')/N = 103.480018.$$

The y moments are of course the same as the x, and we have:

$$r = \frac{S(xy)}{N\sigma_x\sigma_y} = \frac{S(x'y')/N - \nu_x'\nu_y'}{\sigma^2} =$$
$$\frac{S(x'y')/N - A^2}{\mu_2} = .198.$$

Or we may use a short formula for the difference method.[9]

$$r = 1 - \tfrac{1}{2}\frac{\sigma_y{}^2}{\sigma_x{}^2} = 1 - .8024 = .198.^{10}$$

Where σ_y is the standard deviation of the difference between pairs.

Where the number of individuals in an array is very small the method presents no very marked advantages, but when the arrays are large it may be very useful and its range of applicability very wide.

For instance, one of the tests of the genotype theory of inheritance is to compare the correlation between parents and offspring with that between the parents co-fraternity and the offspring in a population of self fertilizing or vegetatively

[8] AMER. NAT., Vol. 44, pp. 693–699, 1910.

[9] Harris, J. Arthur, "A Short Method of Calculating the Coefficient of Correlation in the Case of Integral Variates," *Biometrika*, Vol. 7, pp. 215–218, 1909.

[10] On the basis of $N = 2239$, $r = .198 \pm .014$, and we may conclude that the individual plants are slightly but distinctly differentiated in their capacity for maturing seeds. In his English Series of Broom, Pearson (*Phil. Trans. Roy. Soc. Lond.*, A, Vol. 197, p. 335, 1901) found $r = .42$. The difference may easily be attributed to the smallness of the Woods Hole series, some, or possibly all, of the individuals of which may have come from the same parent plant. The case is an illustration of arithmetical method only.

propagating individuals.[11] The correlation surfaces are very easily prepared. Two seriation tables, one for the arrays from which the individual parents were drawn and one for the offspring arrays corresponding to each parental fraternity, are prepared. The first table is cut into strips by columns, passed strip by strip over the offspring seriation table, the frequencies which are in juxtaposition are multiplied together and summed simultaneously, and the resulting totals entered in the proper compartments[12] of a correlation table. This may be called an ascendant-descendant correlation surface. It includes both "parental" and "avuncular" relationships. The "avuncular" relationship is the one sought, and is quickly gotten by subtracting the surface for the relationship between individual parents and their offspring (which will have been already prepared for other purposes) from the ascendant correlation surface just described.

In a forthcoming paper I shall show how various correlations may sometimes be most easily determined from the first two moments for the individual classes or families without the labor of drawing up tables.

J. ARTHUR HARRIS.

COLD SPRING HARBOR, N. Y.,
July 7, 1911

ACQUIRED CHARACTERS DEFINED

IT is believed that if the term "acquired characters" is carefully defined, and the matter considered in view of that definition, a new light will be cast upon a generally misunderstood subject. The things to be defined are the verb *to acquire*, which means to obtain by effort, and the noun *character*, which means something forming part of an individual. The point of view here involved may be illustrated by the following quotation:

> "Some are born great,
> Some achieve greatness, and
> Some have greatness thrust upon them."

This shows three ways in which an individual obtains greatness. The same three ways apply to the different characters

[11] For an illustration see K. Pearson's analysis of Hanel's data for *Hydra grisea*, "Darwinism, Biometry and Some Recent Biology," *Biometrika*, Vol. 7, pp. 368–385, 1910.

[12] The compartments corresponding to the captions of the two columns dealt with.

which an individual has. Some characters are born in the individual, some are acquired, and some are thrust upon him.

A Roman nose or a pug nose is neither acquired nor thrust upon the individual. They are born to the individuals which possess them. The same is true of gray eyes or blue eyes, and many other characters. They are inborn and are matters of heredity.

A mutilation is not born to an individual or acquired by him. It is thrust upon him by accident or by the action of some other person, and against the will of the individual. A person is not born gray, nor does he achieve grayness. It is thrust upon him by age or by mental distress. We sometimes say that a person acquires a sun-burned face, but the statement is inaccurate. Sunburn is thrust upon the individual by the action of the sun's rays.

Those things which are *acquired* are obtained by the efforts, either physical or mental, of the individual which acquires them. But not all things which are acquired by efforts are "characters." Thus, a person may acquire wealth by his individual efforts, but wealth is not a character. It is a possession. An education is also acquired by efforts, but an education is a possession and not a character. So also athletes and race horses acquire records of various kinds, but these records are also possessions and not characters.

Characters are those things which pertain to and form a part of the individual as an individual. Acquired characters are not new characters, but characters which are changed from their normal inborn condition by their own functional activity, and are to be clearly distinguished from characters thrust upon a passive individual. Using a generic term to cover many specific qualities, it may be said that *strength* is the main if not the sole acquired character under this definition. Weakness is negative strength correlated with negative efforts.

Physical strength above the inherited strength is acquired by special physical efforts, such as training, and mental strength above the inherited mental strength is similarly acquired by special mental training. Conversely, physical strength is lost by the absence of physical efforts, and mental strength is lost by the absence of mental efforts. Efforts are something we can see and measure, and the relationship between these acquirements and the efforts by which they are obtained is such that we can measure the acquirements in terms of efforts.

It has been demonstrated beyond all question that those characters which are thrust upon the individual, such as mutilations, are not inherited. But how about those characters which are not thrust upon the individual but are acquired in accordance with the above definition? That there is a clear distinction between characters which are acquired and those which are thrust upon the individual is evident from the fact that neither mental nor physical strength can be thrust upon the individual. Irritation thrust upon an individual may in fact produce a great display of mental and physical strength, but the circumstance or the person who produced the irritation does not augment the strength which previously existed.

The above analysis shows that the individual after birth does or may come into possession of two kinds of characters, one of which is obtained by acquirement and the other of which is thrust upon him. Also, that those characters which are acquired can not be thrust upon him, and those which are thrust upon him can not be acquired. The distinction between the two kinds of characters is clear cut and marked. Evidence that one of these kinds is not inherited is not even presumptive evidence that the other is not. What is demanded is some clear and precise evidence in regard to those characters which are acquired and can by no possibility be thrust upon the individual.

R. L. Redfield.

NOTES AND LITERATURE

THE PRESENT-DAY CONCEPTION AND STUDY OF ANIMAL PSYCHOLOGY

THE latest issue—or one among the latest issues—in that long series of admirable books called the "Bibliothèque de Philosophie Contemporaine" (Felix Alcan, Paris) is Professor Georges[1] Bohn's "La Nouvelle Psychologie Animale." In 1909 Bohn published his interesting "La Naissance de l'Intelligence,"[2] in which he set out with characteristic French lucidity his position in the field of the new animal psychology, a position based at once on a considerable amount of personal observation and experimentation and on a thorough familiarity with the work of the whole modern school of experimental animal psychologists.

In the present smaller and simpler or more general statement —by general I do not mean vague—Professor Bohn restates with admirable understanding, restraint, definiteness and clearness, the conditions and the conclusions of the modern experimental study of animal reactions of the psychic and pre-psychic order. The conclusions, to be sure, can be held to be those of no other student than Bohn himself until other students give their formal adherence to them. But despite the inevitable disagreements about details, and the reluctance to subscribe to any man's dicta in toto, Professor Bohn's conclusions and attitude will find the adherence of a considerable body of animal psychologists.

The essentials of this position are its strongly "mechanical" tendency, *i. e.*, its attempt to make physics and chemistry and mechanics go as far as possible in explaining both stimuli and reactions; its strong leaning away from finalistic explanations, *i. e.*, the explanations of adaptation and of Darwinian selection; its rather sharp classification into three separate categories of the behavior of the invertebrates less the articulates, the articulates, and the vertebrates, respectively; its conception of these three categories of behavior as standing not as three successive stages in one grand line of evolution, but as of marking three fairly disparate lines of development, that is, of differing not so much

[1] Bohn, Georges, "La Nouvelle Psychologie Animale," pp. 200, 1911, Felix Alcan, Paris, 2 fr. 50 c.

[2] See review by the present writer in *Science*, November 5, 1909.

quantitatively as qualitatively; and, finally, its sharp and clear conceptions of what is meant by tropisms, by differential sensibility, by association of sensations and associative memory.

I have referred to the "strongly mechanical tendency" manifest in Bohn's attitude toward behavior explanations. This is not to align Professor Bohn with those representatives of the extreme mechanical school, such as Beer, Bethe and Uexkull. Recognizing the great service of these men in showing "the errors and the exaggerations" of the anthropomorphic or anthropocentric school of animal psychology, he expressly parts company with them when they push their way to the rigorously logical—or is it illogical?—extreme. Bohn says:

> With the vertebrates the psychic activity acquires, thanks to the brain, a very great complexity. It becomes useless to speak, in their case, of tropisms and of the elementary forms of differential sensibility, for one can no longer isolate these elements from the total activity. The memory has reached a considerable development, and, on the other hand, the chemism has lost its primitive simplicity; each remembrance, each idea can provoke **new forms of sensibility.**

Even with the articulates the "rudiments of associative memory are developed to the point of masking more or less the tropisms and the differential sensibility." Thus by the side of survivals of the older or simpler activities, the articulates reveal new psychic acquisitions due to associative memory.

For the behavior of the lower invertebrates, however, Bohn's explanations hold closely to those of the true mechanical school, those who rely on tropisms and differential sensibility. Bohn is highly appreciative of Loeb's pioneer work, the work that indeed marked the opening of the present epoch in animal psychology study. The originality and genuinely *Bahn-brechend* character of Loeb's work is freely recognized. Indeed, the whole work and activity of the present American school of animal psychology is referred to and praised over and over again in all of Professor Bohn's writings.

"La Nouvelle Psychologie Animale" has been "crowned" by the Académie des Sciences Morales et Politiques. It may also well be crowned by that reading public which likes its science authoritative and yet simple and clear and interesting at the same time.

V. L. K.

STANFORD UNIVERSITY, CAL.

A USEFUL EVOLUTION BIBLIOGRAPHY

THE *Bulletin Scientifique de la France et de Belgique* (founded by Giard and now conducted by Blaringhem, Bohn, Caullery, Mesnil, Perez and others) has begun the issuance of a "Bibliographia Evolutionis" that promises to be of very great usefulness. Now that *L'Année Biologique* is irrecoverably out of date in its annual issues—has it indeed officially expired?—the new "Bibliographia Evolutionis" will be especially welcome.

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The "Bibliographia Evolutionis" apparently may not be subscribed for or purchased separately. To obtain it, then, one must subscribe for the *Bulletin Scientifique de la France et de la Belgique*, 32 francs a year, Redaction du Bulletin Scientifique, 3, rue d'Ulm, Paris. The *Bulletin* is, however, an admirably conducted journal, containing important original papers, by French and Belgian scholars, on evolutionary matters. It is at present in its forty-fifth volume (fifth volume of its sixth series).

Interesting item: the title page of the "Bibliographia Evolutionis" bears on its title page, as stamp of its recognition, a likeness of the face of Jacques Loeb.

V. L. K.

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THE AMERICAN NATURALIST

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MUTATION IN ŒNOTHERA

DR. R. R. GATES

INTRODUCTORY

I HAVE been for some time interested in tracing the history of the various species and races of *Œnothera* from the early records of their introduction into Europe. This method is accompanied with many difficulties which only those know who have attempted it. Conclusions which seem justified in the light of the data in hand sometimes require modification when further records are examined. In a previous note in *Science* ('10), and especially in a longer paper ('11*a*) since published, I have brought together much of the data on which our knowledge of the early introduction of these forms into cultivation must rest.[1] Since that time I have been able to supplement those data by an examination of further records, and particularly of some of the type specimens of these plants in European herbaria. These have confirmed some of my previous conclusions and necessitated modifications of others. Herbarium specimens, where available, are of course the final court of appeal concerning the characters of any plant, but unfortunately they are not infrequently incomplete or even entirely lacking. My examination shows that probably a number of *Œnothera* races existed two or three

[1] Hill ('11) has also briefly discussed the subject and added some data.

centuries ago which are not known to occur in America to-day.

The *O. Lamarckiana* of de Vries's cultures is not the only *Œnothera* which is no longer known to be wild in this country. The same is true of the "European *biennis*" so-called, and of a race of *O. biennis* having very crinkled leaves, which I have cultivated from the Chelsea Physic Garden. It is not sufficiently kept in mind that the collector or species-maker necessarily abstracts. One form, or at best a very few, are selected for seeds or for description as types, from a population containing often a large number of closely allied races; for nature does not select between these races unless the differentiating characters are of value in the survival of the organism, and this appears often not to be the case. In this manner two or three centuries ago various races of *Œnothera* were selected and taken to Europe to be propagated in botanical gardens, but it is evident that many more races were left behind, and since the incoming of civilization some of these have probably disappeared. In nature, among open-pollinated (allogamous) plants (and presumably among a great many animals) there is no such thing as a "pure" species which will breed true in all its characters, showing only purely fluctuating variability. It is only by selecting and inbreeding for a few generations, that we get "pure lines." The only pure lines in nature are to be found among strictly self-fertilized (autogamous) forms. This idea, which has been emphasized by Cook ('07), seems to be too frequently lost sight of in evolutionary studies. The pure line, while a valuable and necessary means of analyzing various problems of heredity, is essentially a laboratory product seldom duplicated in nature among allogamous plants. By continued inbreeding and selection to smaller and smaller differences, races which are more and more uniform may be obtained, as the "pure line" work tends to show. But the natural wild species must (unless regularly self-fertilizing) be looked upon

as an intercrossing population of races, whose appearance is ever changing (within limits) from generation to generation, according to the particular series of crosses or selfings which happen to occur in each generation. Some of the races are likely to fluctuate in numbers or be dropped out entirely as conditions change. The way in which the face of the population changes from one generation to another will, of course, depend upon how the character-differences are inherited, but we need not consider that question here.

It therefore seems to be idle to inquire whether in this sense crossing of the allogamous œnotheras, such as *O. Lamarckiana* and *O. grandiflora,* has taken place, for we must assume that it *has* occurred, in the wild condition as well as in gardens. Our "species" (particularly the earlier ones, when less fine distinctions were drawn than now) are founded upon certain chance combinations resulting from such crosses, which have attracted attention and been abstracted and rendered uniform by continued self-pollination. Nature herself is oblivious of the boundaries between "species" so long as, when crosses occur, the progeny are fertile, and this is frequently the case in *Œnothera.*

I am greatly indebted to Dr. B. Dayton Jackson, general secretary of the Linnæan Society, for the privilege of examining the type specimens of Linnæus's "Species Plantarum," and to Dr. A. B. Rendle and his colleagues of the British Museum (Natural History) for courtesies in connection with the examination of extensive *Œnothera* collections, including the plants of Linnæus's "Hortus Cliffortianus" and various early American collections.

The species of *Œnothera* which need particularly to be accounted for are what we now know as *O. muricata* L., *O. biennis* L., *O. Lamarckiana* Ser. and *O. grandiflora* Ait. Each of these "species" is really an aggregation of a large number of races, differing in many characters but having certain features in common. It

becomes a question how many of these races are to be included in each "species," and it is often a purely arbitrary matter whether the line between two of the species shall be drawn so as to include certain races in one or the other.

As an instance of this I may cite the case of *O. biennis* L. and *O. muricata* L. I have cultivated many wild races of both, including races of *O. muricata* from such localities as Woods Hole, Mass., Gay Head, Mass., Seal Harbor, Me., Middleton, N. S., St. John, N. B., Winnipeg, Man., and St. Paul, Minn. Certain of the races, for instance from St. John and Winnipeg, appeared to be identical, but in most cases they produced uniform races differing constantly in such features as width and color of leaves (varying in different races from very narrow to very broadly lanceolate) and average height of the plant, as well as other characters. The only feature in which all agreed was in certain flower characters, all having a smaller flower than *O. biennis*. In most cases the leaves are also narrower than in *O. biennis*, but as certain races having smaller flowers than *O. biennis* also have broad leaves, it becomes an arbitrary distinction whether these races be included in *O. biennis* on the basis of their broad leaves or in *O. muricata* on the basis of their smaller flowers. The latter course has been followed and they are accordingly classed as *O. muricata* races. On this basis, the only distinction between *O. biennis* forms and *O. muricata* forms is in the size of the flowers, and even this distinction is an arbitrary one. I will not discuss in this connection certain interesting questions relating to the geographical distribution of these races.

My cultures have similarly isolated a number of races of *O. biennis*, some of which differ from each other in most unexpected characters. There is a wide range of variation in flower-size in the different races of *O. biennis*, as there is also to a less extent in *O. muricata*. The general distinction is usually drawn, that self-polli-

nating forms (*i. e.*, those having a short style so that the anthers surround the stigma in the bud) shall be classed as *O. biennis*, and forms with a long style, hence open-pollinated, shall be included in the *O. Lamarckiana* or *O. grandiflora* series of forms. Yet *O. Simsiana* Ser. is a species having large flowers and a short style. The "European *biennis*" has flowers which are larger than any known American races, but it is conveniently classed as *O. biennis* on the basis of its short style. The question as to the characters of the particular plant on which the species name was originally based, also of course enters here. In connection with the early records, herbarium specimens and figures are the chief means of determining approximately the race to which a plant under a given name belonged. The present paper contains the writer's further conclusions concerning these various races and species, and the reader will constantly be referred in this connection to the extensive data already brought together in the paper previously mentioned (Gates, '11*a*).

Early Records and Herbarium Specimens

We may now consider the identity of these various forms in succession. In the paper just mentioned I have given the nine species of *Onagra* listed by Tournefort in his "Institutiones Rei Herbariæ," 1700. Of these the first five are œnotheras. Species number five, *Onagra angustifolia, caule rubro, flore minori,* I have already concluded (*loc. cit.*, p. 87) is our present *O. muricata* L., on the basis of Barrelier's figure (*Lysimachia angustifolia, spicata, lutea, Lusitanica,* fig. 990 in "Plantæ per Gall., Hisp. et Italiam observatæ," 1714). This conclusion is now shown to be correct by Plukenet's figure in the "Almagestum" under the name *Lysimachia lutea, corniculata, angustifolia, flore minore* (t. 202, f. 7), which represents a small-flowered *Œnothera* with narrow leaves. The final proof is given by an examination

of the specimen (probably the one from which the figure was drawn) in Plukenet's "Herbarium," Vol. 96, f. 167, which is in the British Museum. The flowers of this specimen are much smaller than in *O. biennis* and the leaves are narrow, making it evidently a race of *O. muricata*. Linnæus afterwards (quite incorrectly) ("Sp. Pl.," p. 346) combined it with his species *O. fruticosa*. A type of the latter species is a specimen collected by Clayton in Virginia, and is from the herbarium of Gronovius in the British Museum. It represents a race of the modern *O. fruticosa* L. That the error of combining Tournefort's species with this was afterwards recognized is shown by the fact that in an annotated copy of the "Species Plantarum," 2 edition, 1762, in the possession of the Linnæan Society, the citation of "*Onagra angustifolia, caule rubro, flore minore* Tournef. inst. 302" under *O. fruticosa* L. is crossed out. Type specimens of both *O. fruticosa* and *O. muricata* for the "Species Plantarum" are to be found in the Linnæan Herbarium. The latter differs from the type specimen of *O. biennis* (which will be referred to later) in having somewhat smaller flowers, more numerous long hairs on the sepals, narrower and more pointed leaves, and numerous conspicuous murications (long hairs arising from papillæ) on the stem.

We may now take up the consideration of Tournefort's first three species and their synonyms. In my former paper I was strongly of the opinion that species (I) represented a plant which was more closely related to *O. Lamarckiana* than to *O. biennis*, although not identical with any known form, except possibly *O. lævifolia*. The large flowers and quadrangular buds, as well as a consideration of the synonymy, seemed to demand that it be placed with the *O. Lamarckiana* series of forms, rather than with *O. biennis* or *O. grandiflora*. A subsequent examination of certain early specimens has thrown doubt upon this opinion. I have shown (*l. c.*) that the

Lysimachia lutea corniculata of Bauhin,[2] which Tournefort cites as a synonym for his *Onagra latifolia*, is the same plant, or at any rate the same description, as Morison's *Lysimachia lutea corniculata non papposa* and Ray's *Lysimachia lutea Virginiana*. The crucial point in this early synonymy seems to be in Barrelier (1714), who gives rather accurate figures of three species of œnothera, together with their synonymy (see Gates, '11*a*, p. 102). His species (1) is quite certainly a race of *O. biennis*, his species (2) is with equal certainty a race of *O. muricata*, and (3), which has much larger flowers, must, I think, belong somewhere in the series of large-flowered forms represented by *O. grandiflora* and *O. Lamarckiana*. The fact that the name *Lysimachia lutea, corniculata, latifolia, Lusitanica* under which Barrelier figures his species (3) is almost identical with the name *Lysimachia Virginiana latifolia, lutea, corniculata* under which Morison figures *his* large-flowered form (Fig. 7), made it probable that Barrelier's species (3) referred to the same plant as Morison's figure. However, this can not be certain. But I regard it as quite certain that the plant figured by Morison (Fig. 8) under the name *Lysimachia Virginiana angustifolia, corniculata* (see Gates, '11*a*, p. 99) is *O. muricata*. The diameter of the flowers in his Fig. 7 is exactly three times that in Fig. 8. Now Gray's "Manual," ed. 7, gives the length of petals in *O. muricata* as 12–20 mm., in *O. biennis* as 15–25 mm., and in *O. grandiflora* as 40–60 mm., so that the flowers of *O. grandiflora* (or *O. Lamarckiana*) would be approximately three times the diameter of those in *O. muricata*, while even the "European *biennis*" could scarcely reach these dimensions. This appears to be an additional reason for supposing that Morison's larger-flowered plant came in the series represented by

[2] On inquiry from Professor A. Fischer, director of the Botanische Anstalt, Basel, Switzerland, where Bauhin's Herbarium is kept, I find that the specimen of *Lysimachia lutea corniculata*, along with about two thirds of his collection, was discarded as spoiled when the Herbarium was renovated several years ago.

O. grandiflora and *O. Lamarckiana* rather than in *O. biennis*, but as already stated, an argument of this nature can not reach finality. Whether Morison's Fig. 7 represents one of the *grandiflora-Lamarckiana* series or the "European *biennis*," it seems certain that Barrelier's species (3) came in the large-flowered, open-pollinated series represented by *O. grandiflora* or *O. Lamarckiana*.

Unfortunately, the actual specimens in the British Museum, which bear these early names of Tournefort and are supposed to have served as the types for the "Hortus Cliffortianus," are not fully authenticated. The handwriting is said not to be that of Linnæus, and certain differences between the names employed and those which Linnæus himself would probably have used, seem to indicate that they were written by an amanuensis or that some mistake occurred in the naming. This deprives us of certainty in regard to the names they bear. The characters of the specimens themselves are very well preserved. The first specimen (which I shall refer to as specimen 1) bears on the label the name "*Onagra latifolia flore sulphureo*"; the second specimen (2), "*Onagra latifolia*. T. 302," and beneath it is written "*Œnothera octovalvis*." But *O. octovalvis* was a species of Jussieua. These two specimens are identical in every character. They represent evidently a race of the "European *biennis*" having larger flowers than American forms of *O. biennis*, though not so large as *O. Lamarckiana*. The style is short so that the stamens surround the stigma, the buds bear some long hairs, red papillæ occur on the stem, and the leaves are rather broadly lanceolate. The stigma lobes are remarkably long in all the flowers on both specimens. These two specimens may have served as the types of Linnæus's species (1) in Hort. Cliff. (see Gates, '11*a*, p. 102). As far as the characters of these specimens are concerned, they really resemble *O. Lamarckiana* more than they do the American races of *O. biennis*, but are classed with *O. biennis* because the flowers are self-pollinating.

The next specimen (3) in this series is one bearing the label *Onagra latifolia, flore dilutiore* T. 302. As a matter of fact, it differs remarkably little from the two specimens just described. The leaves and stem show no visible difference at all, but the petals appear to have been slightly smaller. The flowers differ markedly, however, in having longer styles, so that the stigma projects some distance beyond the stamens. The stigma lobes are also very short, differing conspicuously in this respect from those of the specimens above. This specimen is something of a puzzle. It was apparently open-pollinated because of its long styles. Yet its flowers were no larger than those of the "European *biennis*." It shows that races may have existed and disappeared, which were quite different from anything we know at present. Whether this form shall be classed with the "European *biennis*" on account of the size of its flowers, or with *O. Lamarckiana* on account of its long style, appears to be an arbitrary matter. Such specimens serve to show that the range of "variability" of these œnotheras in certain directions may have been formerly much greater than would be supposed from a study of those races which have survived to the present day.

Another interesting specimen (4) in this collection is one marked *Onagra latifolia* Tourn. with the date 1743 and a number, 1082. I am indebted to Dr. Rendle for the explanation of the history of this specimen. Sir Hans Sloane contributed to the Herbarium of the Royal Society each year for a number of years, fifty specimens from plants grown at the Chelsea Physic Garden, and these were numbered consecutively. This plant was therefore grown in the Chelsea Physic Garden in 1743. It is apparently the same as specimens (1) and (2) already described as probable types for the "Hort. Cliff." Some of the stem leaves have short petioles and sloping base, others are apparently sessile with broadened base.

The next specimen (5) has the same history as the last. It bears the date 1779 and the number 2878. The

label reads "*Œnothera biennis* foliis ovato-lanceolatis planis, caule muricato subvilloso Lin.: Spec. Plant. 492. *Lysimachia lutea corniculata*. Bauhin: pin. 245." This specimen has smaller flowers than the previous ones, the flowers being the same size as the American races of *O. biennis*. The leaves are very broadly lanceolate, sharply narrowed at base to a very short petiole, and appear to be of a different shape from those of any American *biennis* I have seen. The stem bears scattered papillæ from which long hairs arise.

A consideration of these five specimens makes it highly probable that Tournefort's *Onagra latifolia* and Bauhin's *Lysimachia lutea corniculata* belonged to what we now for convenience call the "European *biennis*" rather than to the larger-flowered, longer-styled, *O. Lamarckiana*. Yet specimen (3) with its long style though the flowers are the same size as in the European *biennis*, makes it impossible to be dogmatic as to where the line is to be drawn between the *O. Lamarckiana* and the *O. biennis* series of forms. If these specimens are correctly labeled, then there must have been comparatively little difference between Tournfort's species (1) and (2), (1) representing the "European *biennis*" and (2) a form probably open-pollinated but with flowers smaller than the present *O. Lamarckiana*. The "long and narrow pale green leaves" of Bauhin's and Parkinson's plant (see Gates, '11*a*, pp. 91 and 95) would indicate that it differed in certain features from any race of the European *biennis* now known.

As already pointed out, the synonymy as well as the flower-size would indicate that Morison's larger-flowered plant *Lysimachia Virginiana latifolia lutea, corniculata* was the same as Barrelier's *Lysimachia lutea, corniculata, latifolia, Lusitanica* which is undoubtedly a large-flowered form. However, it seems on the whole more probable that Morison's plant was the same as Bauhin's, whose description he copies. In any case it seems clear that Barrelier's *Lysimachia lutea, cornicu-*

lata, latifolia, Lusitanica was a large-flowered form belonging in the *grandiflora-Lamarckiana* series, and there is no reason to doubt that his citation of Tournefort's *Onagra latifolia, floribus amplis* as a synonym is correct. It is therefore highly probable that Tournefort's species (3) represents *O. grandiflora*, or perchance *O. Lamarckiana* or some race between these two as we now know them.

The type specimen of Linnæus's *O. biennis* in the "Species Plantarum" (to be found in the Linnæan Herbarium) is, however, not the "European *biennis*," but a smaller-flowered form representing one of the American races of *O. biennis*, having rather narrowly lanceolate stem leaves. I have already pointed out ('11*a*, p. 104) that Linnæus does not cite figures of this form in his synonymy, although a good figure by Barrelier was in existence. Instead he cites Morison's figure which now appears most probably to have been the "European *biennis*," and in the "Hort. Cliff." he cites Barrelier's figure of *Lysimachia lutea corniculata latifolia lusitanica*, which was undoubtedly a large-flowered form.

To summarize briefly the conclusions which seem justified from all the available data, it appears that the earliest introduction, as represented by the plants of Bauhin, Parkinson, Morison and Ray, belonged to a race of what we now know as the "European *biennis*," having flowers larger than the present American races but self-pollinated, although an open-pollinated form with long style appears also to have occurred (specimen 3). *O. muricata* was recognized by Tournefort in 1700, and both *O. muricata* and the "American *biennis*" were figured by Barrelier in 1714, in addition to a large-flowered species which must have been related to *O. grandiflora* or *O. Lamarckiana*. This large-flowered form appears to have been first recognized and briefly described by Ray in 1686 (see Gates, '11*a*, p. 100). Different hypotheses as to the relation between *O. grandiflora* and *O. Lamarckiana* will be considered later in this paper.

O. grandiflora Ait.

In a previous paper ('11*a*, p. 110) I reproduced the manuscript of L'Heritier's description of *O. grandiflora*, which was written about 1788 but was never published. The type specimen of *O. grandiflora* in the British Museum was grown in the garden of Dr. Fothergill in 1778. It has narrowly lanceolate leaves and slender hypanthia, agreeing exactly with some of the plants in my cultures of *O. grandiflora* from Alabama. Solander really did the descriptive work upon this form, and the species should have been given his name instead of that of Aiton. In Vol. IX, p. 387, of the Solander manuscripts, which are in the British Museum, he gives the following additional notes on this plant of Bartram and Fothergill: "(Enothera grandiflora foliis lanceolatis denticulatis villosiusculis, petalis cuneiformibus, calycibus aristatis, pilis caulinis basi tuberculosis. Habitat in America septentrionalis prope Mississippi. Bartram Junr." These characters serve further to identify the plant with the present *O. grandiflora*, the words "petalis cuneiformibus" and "calycibus aristatis" being particularly distinctive.

Evidence from Later Herbarium Specimens.—I may now refer to a number of specimens in the British Museum, which are of special interest for one reason or another. The first of these specimens was marked "*Œnanthera grandiflora* Lin: Willd.," the species name being crossed out and "*longiflora*" written above it. On the back of the page is written "Herb. Demidoff. Pallas." This applies to plants grown by Demidoff in his garden, founded at Moscow in 1756. This specimen differs from the type specimen of *O. grandiflora* in having larger stouter buds, very much stouter hypanthia, larger flowers, leaves narrow but shorter than the type of *O. grandiflora*. It appears to resemble *O. rubrinervis* more than any other form, but has stouter hypanthia than I have ever seen in this mutant.

Another specimen bears the following label: "Bar-

clay. *Œnothera* sp. Shrubby, 3 feet high, flowers yellow. Hab. hilly. Bodegas." This plant from Ecuador has flowers the size of *O. Lamarckiana,* many long hairs on the sepals and young leaves, the leaves being rather narrowly lanceolate, petiolate. The plant must have been very much like *O. rubrinervis,* though differing somewhat in leaf characters. Ecuador is an unexpected place to find plants having these characters.

A very interesting sheet bears the name *O. biennis* L. var. *muricata* Torr. & Gray. It was collected by Dr. Wm. M. Bell, of London, in the Raton Mountains (which extend from southern Colorado to New Mexico) in 1867. There are two specimens and several extra flowers and buds. The flowers are as large as those of *O. Lamarckiana,* the style is long so that the flower is open-pollinated; the hypanthium and bud cone bear numerous long hairs; the buds are the precise size and shape of *O. rubrinervis;* the stem leaves are more narrowly lanceolate than *O. Lamarckiana* but are often broad and sessile at base like that form. This plant is strikingly like *O. rubrinervis* in every particular, except that the upper stem leaves are perhaps a little narrower. The presumption is that these plants were collected in the wild condition, and I have found no reason for supposing otherwise. This would seem to support the view that these *Lamarckiana* forms were formerly found wild in the western region, although it has been suggested that the Texas plants, from which de Vries's cultures appear to have originated, were perhaps descended from garden seeds.

Another very interesting specimen is marked "*Onagra guttata* Greene n. sp., New Mexico, 1904. Alt. 6600 feet." Its leaves are very narrowly lanceolate (much narrower than *O. lævifolia*); the stems red, with many red papillæ bearing long hairs; the flowers are large, style long, and there are many long hairs on the sepals, which also have red bands like *O. rubrinervis.*

These specimens show that forms having large flow-

ers, which belong in the *O. Lamarckiana* series, occur in the western region. One of these specimens is scarcely if at all distinguishable from *O. rubrinervis*. Contrary to the opinion sometimes expressed, I have found herbarium specimens of great value in determining the exact characters of many of these races. There would be no excuse for one familiar with the characters of the plants from cultures, failing to discriminate easily between, for example, *O. grandiflora* and *O. Lamarckiana*, from herbarium specimens showing merely a flowering shoot. And much less conspicuous differences than these, for example in the width or shape of leaves, can be determined with equal accuracy. For example, no one who is familiar with the plants in cultures would confuse typical herbarium specimens of *O. Lamarckiana* and *O. rubrinervis*.

Hypotheses Concerning the Origin of O. Lamarckiana.—There has long been a disposition to look upon *O. Lamarckiana* as a "hybrid"[3] and to suppose that, on this account, the phenomena of the sudden appearance of aberrant types (as described by de Vries), displayed by this form, are necessarily deprived of evolutionary significance. This latter view is one which I do not share. As already pointed out, I consider it necessary to regard open-pollinated forms as hybrids in the sense that their immediate ancestry has been participated in by many races differing in various characters. The germ plasm of such forms is like an unpurified chemical or mixture of chemicals and can only be "purified" by continued self-pollination. This "impure" condition is the one under which the evolution of open-pollinated plants or interbreeding animals goes on, and any assumption

[3] It might be pointed out that the flower characters (which are the crucial characters in many *Œnothera* crosses) of the "European *biennis*" are such as might be expected if it were a "hybrid" between some race of the American *biennis* and some large-flowered form in the *O. Lamarckiana* series. Perhaps it originated as such a hybrid, but the contemplation of the fact is, in itself, of little value for the study of progressive evolution. For practical evolutionary studies, the only universal criterion of a species must be that it breeds true to its peculiarities.

to the contrary merely distorts the facts. If it be assumed that *O. Lamarckiana* is the sudden product of a single cross between two rather more widely separated species, the situation is slightly though not fundamentally changed. As regards *O. Lamarckiana*, the only forms we know which could reasonably be supposed to be its ancestors in this way would be *O. biennis* and *O. grandiflora*, as I have already pointed out (Gates, '11*a*, p. 119). There have doubtless been plenty of opportunities for these species to cross in Botanical Gardens and they have doubtless done so, since the evidence seems clear that certain races belonging to these two "species" were recognized as early as 1686 by Ray as under cultivation.[4] But these species both came from the Virginian region, where there is ample evidence that *O. grandiflora* as well as *O. biennis* originally grew wild, and where the former species was commonly found as late as 1820 (Barton's "Flora of North America," plate 6). Under these circumstances there must have been plenty of opportunities for *O. grandiflora* to be pollinated from *O. biennis* (these forms are visited by moths in the evening when the flowers open), and it would be a bold assumption to suppose that such crosses had not taken place centuries before the white man came to America. Hence if this were the manner of origin of *O. Lamarckiana*, it must have originated in nature long ago. Of course it is well-known that many such species-hybrids are sterile so that when they occur they fail to bridge the gap between species or to take any part in those species' subsequent history and evolution. Assuming that *O. Lamarckiana* originated in this way, its fertility makes its presence in the population of forms of equal im-

[4] I have grown cultures of œnotheras from nearly all the European botanical gardens. The self-pollinating forms are generally quite uniform, while the open-pollinating forms frequently show much variability, which is evidently in part at least the result of crossing. My cultures of *O. grandiflora* from its wild locality in Alabama also show that it contains various aberrant types. On the other hand, it is also true that the self-pollinating *O. biennis* in some localities contains more than one type, but in the case of *O. biennis* it is not probable that these types have arisen through crossing.

portance with that of the two parent species, for it will take an equal part in producing descendants. Furthermore, crossing between the new hybrid forms and the parents will go on indefinitely, producing a host of interbreeding races, and this population will constitute the material for further evolution.

I have been studying this process by means of cultures from seeds of plants on the sand dunes near Liverpool, England, where *biennis*, *Lamarckiana* and *grandiflora* have been interbreeding freely for at least a century, producing a host of races (including several of the mutants of *O. Lamarckiana*), some of which split, but many are found to breed true for at least two generations. It seems to me that the question to ask regarding these races is not as to whether they have originated in connection with crossing, for it is certain that they have originated at least in the presence of conditions in which crossing is taking place in every generation. The question is rather what relation (if any) these races bear to the previous evolution of these forms, whether any of them are progressive in the sense that they will supplant the other races and become the progenitors of future generations, to the exclusion of those which were formerly progenitors. In other words, are the new races progressive in the sense that they show some further development of any character or some new departure in comparison with the parental types, and are they also capable of surviving, propagating themselves and ultimately becoming important elements of the population, from which new races may in turn develop? Does crossing ever lead to the appearance of new and progressive types by the disturbance it produces in the germ plasm, rather than by the mere combination and redistribution of the characters of the forms it brings together? Or is mutation a process apart from any germinal disturbance resulting from crossing? The answers to these questions are often very difficult, but upon these answers depends in large part the status which will ulti-

mately be given to the mutation phenomena in *O. Lamarckiana* as an evolutionary factor.[5]

Is O. Lamarckiana obtained from O. grandiflora × O. biennis?—Before pursuing further the subject of the cause of the mutations in *O. Lamarckiana*, let us examine the hypothesis that *O. Lamarckiana* is the result of a direct cross between *O. biennis* and *O. grandiflora*, for while, since *O. Lamarckiana* must be assumed to have undergone crossing in any case, it is not of vital significance just what those crosses may have been, yet it would be of interest if it could be shown that *O. Lamarckiana* has arisen and can be synthesized, as the result of a single cross. Davis ('11) has recently attempted to produce *O. Lamarckiana* in this manner. His descriptions, however, fail to state the points in the characters of his hybrids, which any one who is familiar with these plants would like to know. Particularly does he omit to state how the bud characters of his hybrids differ from those of *O. grandiflora*. It is stated that the hybrids are in general intermediate between the parent species. This would be expected, at least as regards the flower characters, from the behavior of other hybrids in œnothera, *e. g.*, *O. Lamarckiana × O. biennis*. The flower characters in this cross are nearly intermediate, though resembling *biennis* more than *Lamarckiana*. I have observed closely the flower characters of many crosses, including hybrids between series of forms belonging respectively to *O. grandiflora* and *O. Lamarckiana*, and the flowers are usually intermediate in their characters, though sometimes nearer one parent than the other. If the flowers of Davis's cross are also

[5] It might be assumed that *O. biennis* and *O. grandiflora* were the original forms to become naturalized on the English sand dunes, and that *O. Lamarckiana* has since appeared as the result of crossing between these races. If this is the case, then *O. Lamarckiana* (and many related races which have resulted from further crossing and mutation) has since been successful, under the new conditions, in supplanting the parent forms to a large extent. We should, therefore, in any case, expect these *O. Lamarckiana* forms to become the progenitors of the future generations, and to determine in greater part the future evolution, whatever that might be.

a blend of the parents, as he states ('11, p. 213), then they can not be the same as the flower characters of *O. Lamarckiana*. If, on the other hand, the flowers are as he states, "scarcely distinguishable from those of *O. Lamarckiana*," then they are not a blend of the parental characters.

I have previously pointed out the differences between *O. grandiflora* and *O. Lamarckiana* (Gates, '99*a*, pp. 131, 132) and Miss Vail (in MacDougal, Vail and Shull, '07, p. 66) has described the characters of *O. grandiflora* in detail. For convenience, the flower differences between *O. biennis*, *O. grandiflora* and *O. Lamarckiana* may be summarized here. *O. biennis* has small flowers, in which the stamens surround the stigma in the bud. The anthers are in contact with the stigma in the bud and are ruptured before the bud opens, so that when the opening of the flower occurs, and the anthers move away from the stigma, viscous strings of pollen are found running from each anther to a lobe of the stigma in the newly opened flower. Self-pollination thus invariably takes place in *O. biennis*. In neither *O. Lamarckiana* nor *O. grandiflora* does this happen, for the reason that the style is longer so that the stigma lobes, instead of being surrounded by the anthers, are projected above them. The anthers are ruptured as early as in *O. biennis*, but not being in contact with the stigma lobes, the strings of pollen seen in the opening *biennis* flower never occur in *O. Lamarckiana* or *O. grandiflora*. If, as Davis states (see *l. c.*, p. 216), the anthers in *O. Lamarckiana* touch the lower part of the stigma lobes, then these strings of pollen and self-pollination would occur. But this condition is not found in *O. Lamarckiana*, though it does occur (as would be expected) in the hybrid *O. biennis* × *O. Lamarckiana*.

As regards the size of the flower, the statements of Davis also need some revision. He assumes that the flower of *O. Lamarckiana* is smaller than that of *O. grandiflora*, whereas the *O. Lamarckiana* of my cultures

is on the average somewhat larger than *O. grandiflora* from Alabama grown under the same conditions. The same thing is shown by the measurements of Miss Vail. I should first point out that in all the œnotheras the flowers in the early part of the season are uniform in size, but towards the latter part of the blooming-season, with dwindling vitality they steadily decrease in size until the latest-blooming flowers in *O. Lamarckiana*, for example, have petals no larger than *O. biennis*. The style in *O. Lamarckiana* does not, however, decrease in length at as fast a rate as the petals, the result being that in late-blooming flowers it not infrequently protrudes from the unopened bud. But there is no time in *O. Lamarckiana* (in my cultures) when the "base of the stigma lobes is slightly below the tips of the anthers." Davis's Fig. 18 ('11) is misleading as a typical flower of *O. Lamarckiana*, its petals being much too small. He states (p. 216) that the hybrid whose flowers are "scarcely distinguishable from those of *O. Lamarckiana*" has petals 2.2 cm. long. By choosing flowers towards the end of the blooming-season it will be possible to find petals of any desired size, down to that of *O. biennis* itself, but in stating the size of petals for comparison with *O. grandiflora*, it is only fair to choose the typical flowers which are characteristic of the greater part of the season, and which *O. biennis* never produces. MacDougal ('03) states the length of the petals in *O. Lamarckiana* to be 4–5 cm., and Miss Vail in *O. grandiflora* ('07, p. 66) 3.5–4.0 cm., which agrees with my cultures, while in Gray's Manual the petals of *O. grandiflora* are given as 4–6 cm. In my cultures the flowers of *O. Lamarckiana* have been certainly not smaller, but on the whole larger, than in *O. grandiflora*. *O. Lamarckiana* is therefore not intermediate between *O. biennis* and *O. grandiflora*, either in length of style (though the style may sometimes be *slightly* shorter than in *O. grandiflora*) or size of petals, but is almost in agreement with *O. grandiflora* in both these characters. As already pointed

out, the petals of *O. grandiflora* are also characteristically narrower and more cuneiform than in *O. Lamarckiana*, though this is not always the case.

In a number of other flower characters *O. Lamarckiana* is more in agreement with *O. biennis*, and contrasted with *O. grandiflora*. Both the first-named species have quadrangular buds with a prominent median ridge on each sepal, while in *O. grandiflora* the buds are rounded and the median ridge much less prominent. Also these two species agree in bearing on the sepals, hypanthium and ovary a conspicuous long, pointed type of trichome arising each from a papilla and giving the bud a rather strongly pubescent appearance;[6] while this type of hair is, in my experience, always absent from the buds of *O. grandiflora*, which therefore have a glabrous appearance, although a small inconspicuous type of hair is often present, as is the case always in the other two species. *O. biennis* and *O. Lamarckiana* also agree in having rather thick sepals and rather stout sepal tips, while in *O. grandiflora* the sepals are thinner and more delicate, and the sepal tips longer and more setaceous. These differences give the buds of *O. grandiflora* a very different appearance from those of *O. Lamarckiana*, so that even in ordinary herbarium material there is not the slightest difficulty in distinguishing them.

These contrasting flower characters are brought together for greater convenience of reference, in the table below:

FLOWER CHARACTERS		
O. biennis	*O. Lamarckiana*	*O. grandiflora*
Petals 12–16 mm. long.	Petals 40–50 mm. long.	Petals 35–40 or 60 (?) mm. long.
Stigma surrounded by the anthers, invariably causing self-pollination before the bud opens.	Stigma lobes above the anthers, so that self-pollination in the bud does not occur, though the style may be *slightly* shorter than in *O. grandiflora*.	Stigma lobes above the anthers, so that self-pollination in the bud does not occur.

[6] In some races of *O. biennis* there is instead an intermediate type of trichome arising from the even surface of the buds.

Buds quadrangular.	Buds quadrangular.	Buds rounded.
Buds bearing two types of hairs, (1) a short, delicate type, (2) a long, pointed type arising from papillæ and giving the bud a pubescent appearance.	Same as *O. biennis*.	Buds bearing only type (1), or sometimes entirely free from hairs. Type (2) is never seen to occur on the buds of this form, unless previously crossed with *O. biennis* or *O. Lamarckiana*.
Sepals rather thick and sepal tips rather stout.	Essentially the same as *O. biennis*.	Sepals thinner and sepal tips more setaceous.

Thus *O. Lamarckiana* agrees with *O. biennis* in certain features of the flowers, while agreeing equally with *O. grandiflora* in certain other features. We know that these three species when crossed give more or less blended or intermediate hybrids, as appears to be frequently the case in crosses between "Linnæan" species.[7] This being the case, we should not expect to derive *O. Lamarckiana* from a cross between the ordinary races of *O. biennis* and *O. grandiflora*, for this would imply alternative rather than blended inheritance of the various flower characters. Davis has not taken into account the important differentiating features between the buds of *O. Lamarckiana* and *O. grandiflora*, merely telling us that the "inflorescence was very similar to *O. Lamarckiana*," and that "the only essential difference between the buds lay in the slightly greater attenuation of the sepal tips." But his hybrids can not be, as he states, and as would be anticipated from the results of similar crosses in œno-

[7] In an extensive series of crosses between *O. Lamarckiana* and *O. grandiflora* races, the results of which can not be presented here, the flowers of the F_1 are shown to be, in many cases, at least, a blend of the parents. The buds are less conspicuously quadrangular than in *O. Lamarckiana*, the sepal tips more slender, and the long type of hair is about half as numerous. The casual observer would consider these buds to be the same as in *O. Lamarckiana*. Closer inspection, however, shows that this is not the case. In certain of these crosses, however, a type occurs in the F_1 having buds which closely resemble *O. grandiflora*.

thera, a blend of the parental characters, and at the same time agree with *O. Lamarckiana.*

Similarly, in the description of the foliage of his hybrids, Davis fails to take into account the leaf-differences involved. *O. grandiflora* agrees with most American races of *O. biennis,* in having stem-leaves which are lanceolate and tapering at both ends, forming a petiole. In *O. Lamarckiana* the stem-leaves are, on the contrary, usually sessile and broad, almost clasping, at the base, in addition to being crinkled.

A form which would resemble *O. Lamarckiana* much more closely than the hybrids of Davis, could doubtless be synthesized by using a race of *O. biennis* which I have cultivated from seeds obtained from the Chelsea Physic Garden. This race differs strikingly from any other race of *O. biennis* I have seen, in having stem-leaves sessile, very broad at base and very much crinkled. If such a race were crossed with *O. grandiflora,* hybrids might be expected whose foliage at least would closely resemble that of *O. Lamarckiana,* though the flowers would probably be intermediate between *O. Lamarckiana* and *O. biennis.*

One feature which has always made it appear improbable that *O. Lamarckiana* originated as the result of the single cross *O. grandiflora* × *O. biennis,* is the way in which the mutants of *O. Lamarckiana* all agree with that form in certain characters; and not one of them, so far as I am aware, shows any indication of a reversion towards either *O. biennis* or *O. grandiflora.* That the mutants all have certain features in common, which they do not share with *O. biennis* or *O. grandiflora,* and that all may be grouped around *O. Lamarckiana,* was shown in my analytical key to these forms (Gates, '09*a*, pp. 126, 127). While there are wide departures from *O. Lamarckiana* in many characters, in no case does this appear to bring them nearer either *O. biennis* or *O. grandiflora* races. It is difficult to understand why this does not occur, on the theory that *O. Lamarckiana* is such a

simple hybrid.[8] These facts that, so far as now known, *O. biennis*, *O. Lamarckiana* and *O. grandiflora* all behave alike in crosses with each other (that is, they give blends), together with the fact that none of the mutants revert towards either *O. biennis* or *O. grandiflora*, have always seemed unfavorable to the view that *O. Lamarckiana* has originated suddenly from such a single cross. On the other hand, it by no means follows that *O. Lamarckiana* or various other species of *Œnothera* could not be produced by sufficient crossing of races under suitable conditions. My studies of a colony of œnotheras from the English sand dunes, show that numerous races which breed true and have numerous entirely unanticipated characters (often differing from each other conspicuously in every organ) can be obtained as the result of indiscriminate crossing. Some of these races when crossed give blends and have thus far defied Mendelian analysis. I have been able to synthesize at least one of these true-breeding forms by crossing of races. A number of the other peculiar constant races have doubtless had a similar origin, though too complex to be easily repeated. The character-differences of these races do not *appear* to be Mendelian and the races come true except for varying percentages of "mutants."

The mutants of *O. Lamarckiana* themselves, when crossed with their parent form, show apparently a different type of behavior from the species, but that is a matter I will not enter into in the present paper.

How do the Mutants of O. Lamarckiana Originate?—Tower's experience ('10, p. 315) in crossing species of *Leptinotarsa* and thus synthesizing a new race which breeds true except for sporadic "mutants," appears to

[8] In my cultures of œnotheras from the sand dunes of the coast of England, I have obtained occasional mutants having many of the flower-characters of *O. biennis*. But in this case there was abundant opportunity for recent crossing with *O. biennis* to have taken place, and this would seem to be the most probable explanation of their occurrence. I have more recently seen similar occurrences in forms from botanical gardens which have obviously undergone much crossing.

be similar to the behavior just described, and increases the probability that *O. Lamarckiana* may have had a similar origin in nature and perhaps also in gardens. As already pointed out in this paper, it must be assumed that *O. Lamarckiana* has undergone crossing which has determined its present characters, and that its ancestry is therefore "impure." Whether it has resulted from any particular cross is of less interest from the evolutionary standpoint. As I have tried to show in the introduction to this paper, it probably must be conceded that the mutations of *O. Lamarckiana* are connected with previous crossing in the ancestry. This crossing was accompanied by a disturbance of the germ plasm, such disturbance manifesting itself in the occasional production of various aberrant types displaying whole series of new characters. But there are certain reasons why the resulting "disturbance" appears to be something more than a case of hybrid splitting. I shall not go into the details of this question in the present paper, but I may point out one or two facts. Even if (as is quite possible) certain mutants, such as *O. lata* and *O. nanella*, which are evidently retrogressive forms, could be so accounted for; there are at least two forms which could not be brought into this category. The first of these is *O. gigas* with its tetraploid number of chromosomes and a new series of characters, in part, no doubt, the result of the chromosome doubling. I ('09*b*) have suggested that this origin is probably similar to that of many tetraploid species in nature. Ordinary hybrid splitting will not account for it.

Another mutant which is clearly positive or progressive, and which can not be explained as a result of hybrid splitting, is *O. rubricalyx*, which appeared in my cultures in 1907 as a mutant from *O. rubrinervis*, showing a great increase in anthocyanin production (see Gates, '11*b*, for an account of its behavior). These two cases alone make it necessary to assume that "muta-

tion'' is due to a more general disturbance of the germ plasm than would occur in hybrid splitting.

The mutation process, therefore, while probably a result of previous crossing in the ancestry of *O. Lamarckiana*, is not a simple case of the splitting off or reappearance of types which entered into that ancestry. It is probable that much of the hybridization-behavior of the genus *Œnothera*, including particularly crosses which involve the mutants of *O. Lamarckiana* as one of the parents, will ultimately be harmonized with Mendelian categories.[9] But it is also probable that the appearance of the ''mutants'' of *O. Lamarckiana* is not a case of Mendelian splitting as we understand that process at present. The origin at least of such mutants as *O. gigas* and *O. rubricalyx* can not be explained on this basis, and at present can only be ascribed to a general disturbance or condition of instability, which probably resulted from previous crossing. The change in climate to which *O. Lamarckiana* has been subjected may also very well have had something to do with this disturbance, although this is less probable since this plant when brought back to America continues to exhibit the same mutation phenomena.

I have tried to show (1) that *O. Lamarckiana*, like other allogamous forms, has undoubtedly undergone crossing in its ancestry, and (2) that, whatever may have been the relation between these crosses and the appearance of mutants, the important matter to decide from the evolutionary standpoint is, Will these forms survive in nature and become the starting points for new races? As regards *O. gigas*, I have pointed out (Gates. '09*b*) many cases among plants, of species which have probably originated in an analogous manner.

There is one further phase of the mutation process

[9] A recent paper of Miss Saunders (''Studies in the Inheritance of Doubleness in Flowers—I, *Petunia*,'' *Journ. of Genetics*, I, 57–69, 1910) makes it probable that some at least of the alternative inheritance in crosses between *O. Lamarckiana* and its mutants will find an explanation in this way.

which I may touch upon very briefly. That is, the exact method of origin of the various mutants, from the cytological standpoint. It is now certain that the nature of the change involved is not the same in all cases. In the case of *O. gigas*, the most striking change, which brought with it many size changes, is the doubling in the chromosome number. This most probably occurred either in the fertilized egg or in the megaspore mother cell, which then developed apogamously (Gates, '11*c*). On the other hand it seems most probable that several other mutants are the results of changes occurring during the reduction divisions. All the retrogressive mutants may be accounted for in this way, as I have shown (Gates, '08), as the results of occasional irregularities in the distribution of members of the chromosome pairs, if we assume the chromosomes to differ in their chemical activities. *O. rubricalyx* again is a mutant from *O. rubrinervis* in which a marked *quantitative* change in one character (namely, capacity for anthocyanin production) has taken place. We have here the mutational appearance of a new dominant character. A change of this kind is not likely to be concerned with a new chromosome distribution, but is perhaps due to a cytoplasmic difference. As far as can be determined, the external conditions under which this mutant appeared and developed differed in no way from those of the rest of the culture, although it is impossible to deny that some local soil-difference might possibly have actuated this germinal change. This would, however, necessitate the assumption that the change took place in the germinating seed.

Mutation appears, therefore, to be not a simple unitary process of splitting, but to be the result of a condition of instability in the germinal material, which is again probably a result of previous crossing, and which leads to various types of departure from the parental race. That this process will account for much species-formation, and the polymorphism of many genera, can

not be doubted; but it is not clear that adaptation and the larger evolutionary trends can be sufficiently accounted for in this way, although occasional real germinal advances are seen to occur.

Summary

It must be assumed that crossing has taken place in the ancestry of *Œnothera Lamarckiana,* as well as in all forms whose flowers are open-pollinated. Among open-pollinated plants (and the same is probably true of animals) there is no such thing as a "pure" species, but rather, many interbreeding races whose combinations vary from generation to generation make up the population.

Further studies of historical records, and particularly of early herbarium specimens, make it probable that the "European *biennis*" so-called, rather than *O. Lamarckiana,* was the first *Œnothera* introduced into Europe. Herbarium specimens show, however, that forms closely resembling if not identical with *O. Lamarckiana* and *O. rubrinervis,* formerly occurred wild in the western region of Colorado and New Mexico, and that other forms which, from their flower characters, must be closely related to *O. Lamarckiana* also occur there even now.

Granting that *O. Lamarckiana* must have undergone crossing in its ancestry, it does not necessarily follow that it has been synthesized by a single cross, such as *O. grandiflora* × *O. biennis.* The fact that the characters of the parents are usually blended in crosses between Linnæan species of *Œnothera,* while *O. Lamarckiana* agrees with *O. biennis* in certain bud characters and with *O. grandiflora* in certain other flower characters, does not favor the hypothesis that *O. Lamarckiana* originated from this cross; and the evidence offered by Davis is not supported by a sufficiently critical study of the characters of the three species concerned, the flowers of his hybrids being little more than half the size of ordinary *O. Lamarckiana* flowers. By selecting certain other

races of *O. biennis* for crossing with *O. grandiflora*, hybrids more closely resembling *O. Lamarckiana*, at least in foliage, could doubtless be obtained. It would appear that, as far as the characters are concerned, the "European *biennis*" is as likely to have originated by a cross between *O. biennis* and *O. Lamarckiana*, as *O. Lamarckiana* is to have originated from *O. grandiflora* × *O. biennis*.

From the evolutionary standpoint, however, the important question is not whether a given "species" has arisen through crossing, because this is the condition under which the evolution of open-pollinated species must have taken place. Whether or not we assume that mutation is the result of previous crossing, it is necessary to determine whether the new types which appear are progressive and will form races which will become in turn the progenitors of future types.

Even if it be assumed that *O. Lamarckiana* originated from a cross between *O. grandiflora* and *O. biennis*, such crosses must have occurred in nature in North America centuries before the advent of the white man. For there is ample evidence that both these species originally occupied the Virginia-Carolina region.

The natural and necessary tendency of systematists and collectors is to abstract a few from many existent types, as the foundation for their species. The result is that the actual limits between Linnæan species appear well-defined until the discovery of intermediate races bridging such gaps makes it appear that, in many cases at least, the lines drawn between Linnæan "species" are purely arbitrary. This is shown by cultures of many races belonging to *O. biennis* L. and *O. muricata* L. from various parts of North America.

One piece of negative evidence which does not favor the hypothesis that *O. Lamarckiana* originated from *O. grandiflora* × *O. biennis*, is the fact that none of the mutants from *O. Lamarckiana* have hitherto shown any tendency to revert to either of the putative parents. but

rather, all seem to agree with *O. Lamarckiana* in a certain constellation of flower characters. From plants from garden seeds, however, which have evidently undergone crossing (*e. g.*, *O. suaveolens* from the Nantes Botanical Garden), I have occasionally obtained "mutants" with large petals and short styles.

It seems that the mutation phenomena in *O. Lamarckiana* are due to a disturbed or unstable condition of the germ plasm, which has probably resulted from crossing in the ancestry. It is not probable, however, that the retrogressive mutants, such as *O. nanella* and *O. lata* are due to simple hybrid splitting of types which entered into the ancestry. The chromosomal irregularities during meiosis (maturation), which I described, furnish a possible basis for the occasional appearance of retrogressive mutants in each generation.

Certain cases, however, can not be explained as the result of hybrid splitting or loss of characters, and show that *O. Lamarckiana* has experienced a more general disturbance of its germ plasm. Of these cases, *O. gigas* with its tetraploid number of chromosomes, probably originated through a germinal change at another point in the life cycle. A number of tetraploid species among angiosperms and ferns have probably originated in an analogous manner. Also *O. rubricalyx*, a mutant from *O. rubrinervis* showing a large positive variation in red pigment productions, is not likely to have originated through a new chromosome combination, but more probably through some quantitative cytoplasmic change.

Mutation in *O. Lamarckiana*, therefore, appears to be a condition of germinal instability and not a simple process of hybrid splitting, although this condition of instability has probably been brought about through previous crossing in the ancestry. There is, however, at present no satisfactory evidence that *O. Lamarckiana* has originated from a single cross.

Mutation, whether or not always preceded or accompanied by crossing (of which it is probably a result),

will thus account for much species formation, and for the polymorphism of many genera. That it will account for the larger evolutionary trends and for many adaptations, remains to be shown.

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SOME EXPERIMENTAL OBSERVATIONS CONCERNING THE BEHAVIOR OF VARIOUS BEES IN THEIR VISITS TO COTTON BLOSSOMS. I

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In the past a great deal of experimental work has been carried on to determine how flowers attract insects. The conclusions reached have been various and have served to provoke lively discussions as to the relative importance of the visual sense and the olfactory sense in guiding insects to flowers.

Beginning with the notable work of Sprengel, an extensive literature has developed attempting to explain the relative importance of colors and odors in attracting insects to flowers. The conclusions reached have served to provoke lively discussions as to the relative importance of the visual and olfactory sense in guiding insects to flowers. Herman Müller, Delpino, L. Errara, Lubbock, Knuth and others firmly supported the view that flowers advertised their location to passing insects by their conspicuous colored portions and considered odors of only secondary importance. In 1879 Gaston Bonnier advanced the opinion that colored petals were of slight importance in attracting insects to flowers. Later, after much experimenting, Felix Plateau promulgated his extreme views that the colored structures of blossoms were of practically no use as a means of attracting insect visitors, but that odors were the chief means by which bees and other insects were led to find blossoms. Plateau radically expressed himself as follows:

Dans les rapports entre les insectes fécondateurs et les fleurs entomophiles la coloration plus au moins vive des organes floraux n'a pas le rôle prépondérant que Sprengel, H. Müller et leurs nombreux adeptes lui ont attribué. Toutes les fleurs de la nature pourraient être

vertes comme les feuilles sans que leur fécondation pas les insectes fut compromise. L'odorat si développé chez la plupart des insectes loin d'être un facteur accesoire est vraisemblement le sens principal qui leur fait découvrir les fleurs renfermant du pollen ou du nectar.[1]

It is pretty generally conceded, however, that the corolla of flowers and many other conspicuous floral structures possess a very important function in serving to attract various insects. Many odors likewise serve the same purpose, even to a very considerable extent, as shown by the interesting experiments of Plateau and others.

In connection with experimental cotton breeding investigations in northern Georgia, the writer has had occasion to give considerable attention to the visits of bees and other insects among cotton blossoms in this region. The large number of certain species of bees regularly visiting cotton blossoms and the ease with which observations could be made in the field led the writer, during the summer of 1910, to make a series of experiments in order to learn more definitely, if possible, just how cotton blossoms attract bees, whether mainly through the visual or the olfactory sense.

These experiments were made at the beginning of the blooming season when blossoms were very scarce and bees very numerous. The first experiment was begun in the forenoon of July 26, and others followed throughout July and early August. Each day the period of observations began at eight or nine o'clock and terminated about twelve or one o'clock, at which time the blossoms were beginning to close and bee visitors were much less frequent. For each test a period of half an hour or an hour was usually allowed, thus making the number of insect visits sufficiently numerous for valid conclusions.

By far the majority of bee visits were made by *Melissodes bimaculata*, although other species of *Melissodes* were no doubt casual visitors. The big wasp (*Elis plumipes* Drury) and a *Bombus* or an *Entechnia* occasionally

[1] "Les Insectes et la Couleur des Fleures," *L'Année Psychologique*, 13, 1907.

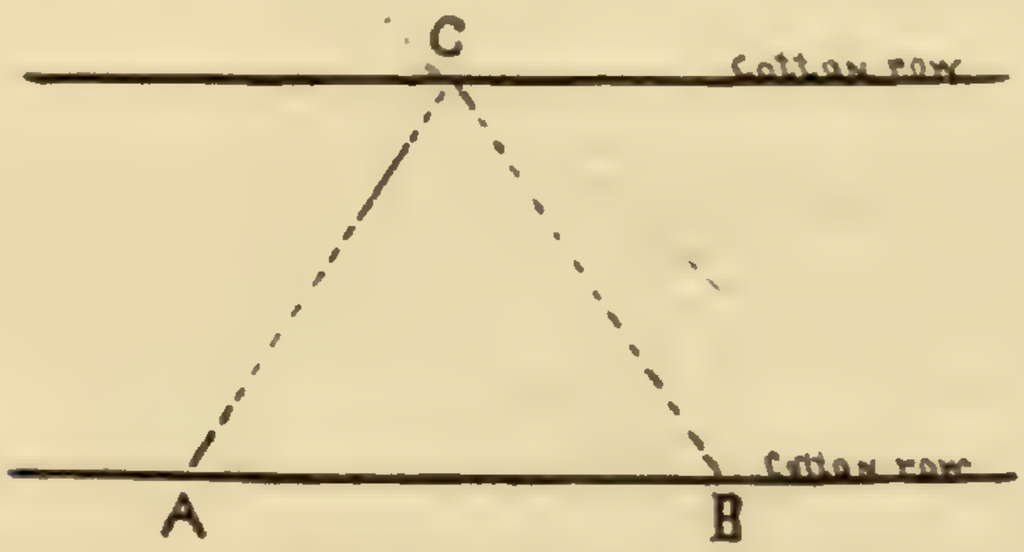
appeared. Later in the season the visits of the extremely common *Melissodes bimaculata* suddenly fell off, and the common honey bee (*Apis mellifica* L.) became more frequent in its visits. For reasons rather difficult to explain, honey bees at the beginning of the experiments were very rare visitors.

The observations and conclusions apply mainly to the behavior of species of *Melissodes*. A count was made of every bee which gave definite evidence that it had perceived the blossoms under observation. These records also included the number of times bees actually alighted upon or entered them. Many bees which do not enter a blossom frequently indicate that they have perceived it by a sudden pause or quick turn toward it momentarily. The manner and thoroughness of these inspections by bees ranges from the merest swerve and hesitation in their flight to a close and scrupulous scrutiny of the blossoms from all sides as they hover over them. At all times it is evident that the actual number of entrances into a blossom is small when compared with the number of inspections without entering. Just why so many bees inspect a normal blossom and refuse to enter is not clear. This is more particularly the rule with species of *Melissodes*.

It is not long till one can readily identify the more important bee visitors within certain limits by their different flight characteristics. Bees of the species *Melissodes bimaculata* appear as black, swift-flying, nervous bees, and are readily determined by their hasty movements among the cotton plants. The species of bumble bees, the common honey bee and *Elis plumipes* are more labored in their flights from blossom to blossom. The wasp, *Elis plumipes*, usually flies very slowly and seems to find it necessary to alight on a blossom in order to inspect it to advantage.

At the beginning of the experiments three blossoms were arranged in such a way as to form a triangle were they connected by straight lines. In some of the

later tests the blossoms were arranged in a line on the same row of cotton. When the triangular arrangement was followed, the points (*a*) and (*b*) were on plants in the same row and about four feet apart. Point (*c*) was situated on the next row back, equally distant from (*a*) and (*b*). The writer was concealed in the cotton directly in front of these points so that each could be kept readily under observation at all times (see Fig. 1). In each test



the only changes made were concerned with the blossoms at the points in question. One blossom at least in each experiment served as a control. See the accompanying triangular diagram.

Experiment No. 1.—July 26. Time of observation, one hour—from 9 to 10 A.M.

At (*a*) a normal blossom was growing *in situ* as a control.

At (*b*) a normal blossom was growing *in situ* as a control.

At (*c*) petals only of a blossom were carelessly pinned to a stem.

An *Elis plumipes* once alighted on the petals of (*c*), but immediately discovered the deception and flew away. The species of *Melissodes* in no instance alighted. These bees, it would seem, possess rather keen discerning powers, since without alighting they quickly detect the difference between a normal and a mutilated flower. In many instances, however, they inspect very carefully

a suspicious blossom before passing on. From this test it is evident that the petals alone, as used at (*c*), were quite as efficient in inviting inspection as the normal blossoms themselves. The blossom at (*b*) received fewer inspections, probably because it was less readily perceived among the leaves which nearly surrounded it.

The bee visits were distributed as follows:

DATA FOR EXPERIMENT NO. 1

Points of Triangle	Total Inspections	Distribution by Species					Total Entrances	Distribution by Species				
		Melissodes sp.	*Elis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Elis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	81	77	1			3	6	3	1			2
(*b*)	44	44					4	4	0			
(*c*)	82	81	1				0	0	0			

Experiment No. 2.—July 26. Time of observation one half hour, from 10 minutes past 10 to 10:40 A.M. Blossoms in the triangular arrangement as before. See diagram.

At point (*a*) same blossom with petals removed.

At point (*b*) same blossom entire as a control.

At point (*c*) petals alone as in preceding experiment.

DATA FOR EXPERIMENT NO. 2

Points of Triangle	Total Inspections	Distribution by Species					Total Entrances	Distribution of Species				
		Melissodes sp.	*Elis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Elis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	4	4					0					
(*b*)	50	50					5	5				
(*c*)	62	62					0	0				

The removal of the corolla of (*a*), which in the past experiment received 81 inspections, reduced the number of inspections at once to 4 as compared with 62 inspections of the detached petals at (*c*).

Exactly similar results were obtained by Darwin in

his experiments with *Lobelia erinus*. He says: "I cut off the petals of some and only the lower striped petals of others and these flowers were not once again sucked by the bees, although some actually crawled over them. The removal of the two little upper petals alone made no difference in their visits."

Experiment No. 3.—July 26. Time of observation one half hour, from 10:40 to 11:10 A.M. Blossoms in the triangular arrangement.

At point (*a*) 3 petals are replaced loosely.

At point (*b*) same blossom entire as before. Control.

At point (*c*) petals alone as in preceding experiments.

DATA FOR EXPERIMENT NO. 3

Points of Triangle	Total Inspections	Distribution by Species					Total Entrances	Distribution by Species				
		Melissodes sp.	*Elis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Elis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	53	51			2		0					
(*b*)	51	50			1		1				1	
(*c*)	67	65			2		0					

With these petals now carelessly affixed to the blossom at (*a*) from which the corolla had been entirely cut away, the number of inspections is at once as frequent as for the control at (*b*). It appears that color and texture more than normal form and arrangement first direct the bees to inspect the blossoms.

Experiment No. 4.—July 26. Time of observations one half hour, from 11:15 to 11:45 A.M. Blossoms in the triangular arrangement with the following change from the preceding experiment.

At (*a*) cloth petals of an artificial rose are carefully arranged and pinned in position to simulate an open cotton blossom. The color of those petals approximated the creamy yellow of a natural cotton blossom; the texture, however, was very different.

At (*b*) control. Same blossom entire as in the preceding experiment.

DATA FOR EXPERIMENT NO. 4

Points of Triangle	Total Inspections	Distribution by Species					Total Entrances	Distribution by Species				
		Melissodes sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	6	6					0					
(*b*)	48	45			1	2	9	7				2
(*c*)	65	62			1	2	0					

At (*c*) control. Petals only as in the preceding experiment.

Bees have been very little attracted by the artificial cloth petals at (*a*). Although the color is not precisely that of a cotton blossom, several bees gave evidence of having perceived them. The texture, which is that of coarse meshed cloth, is quite unlike that of cotton petals, however, and may have been readily perceived as unreal by the bees. The few inspections were without doubt invited by the color of the artificial petals, since no odors could be considered operative unless of a repellent nature.

Experiment No. 5.—July 26. Time of observation one half hour, from 11:45 to 12:15 A.M. Blossoms in the triangular arrangement with the following changes:

At (*a*) five cotton petals (normal number) are carelessly placed over the artificial cloth petals.

At (*b*) control. Same blossom entire as in the preceding experiments.

At (*c*) petals alone as in the preceding experiments.

DATA FOR EXPERIMENT NO. 5

Points of Triangle	Total Inspections	Distribution by Species					Total Entrances	Distribution by Species				
		Melissodes sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(a)	48	45				3	1					1
(b)	44	43				1	7	7				
(c)	50	48	1			1	0					

It is now evident that all the blossoms serve equally well to invite inspection. It is plainly indicated that the artificial cloth petals could have possessed little or no repellent odor, although they received very few inspections in the experiment just preceding. It is not improbable that the different texture of the material revealed the artificial nature of the cloth petals to the bees.

Experiment No. 6.—July 27. Day cloudy, showery in forenoon, thus greatly interfering with frequency of visits. Blossoms in the triangular arrangement.

At (*a*) control. A normal blossom pinned in position.

At (*b*) control. A normal blossom growing *in situ.*

At (*c*) a single petal pinned to a stem.

Observations were begun at 9:00 A.M., but rain intervened at 9:15. A single inspection was recorded for (*c*).

Observations were again begun at 10:25, lasting for one half hour until 11:05. The blossoms were arranged in the triangle as follows:

At (*a*) control. A normal cotton blossom pinned in position.

At (*b*) control. A normal cotton blossom growing *in situ.*

At (*c*) a half opened bud simulated by pinning normal petals together, the calyx being represented by a portion of a green cotton leaf carefully wrapped around the base. In this way it was absolutely certain that no unaccustomed odors were introduced. This bud-like arrangement prevented all chances of examination of the inner details by bees until they had actually squeezed down between the petals.

DATA FOR EXPERIMENT NO. 6

Points of Triangle	Total Inspection	Distribution by Species					Total Entrances	Distribution by Species				
		Melissodes sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Epiblumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	48						2					
(*b*)	21						0					
(*c*)	47						1					

A record of the kind of bees was not accurately kept, but species of *Melissodes* were almost the only visitors. The blossom at (*b*) was less visible than those at (*a*) or (*c*), both of which were in plain view of each other. The blossom at (*b*) was not visible either from (*a*) or (*c*), so that many bees which inspected (*a*) and (*c*) frequently failed to perceive (*b*).

Experiment No. 7.—July 27. Period of observations one half hour from 11:08 to 11:38. Blossoms in the previous triangular arrangement changed as follows:

(*a*) Normal blossom used in the preceding experiment concealed by fastening the surrounding leaves in such a manner that the blossom would be visible only by bees passing directly over it.

(*b*) Control. Normal blossom growing in situ.

(*c*) Artificially constructed bud as used in latter half of experiment 6.

The inspections were as follows:

(*a*) Received a single inspection from a bee flying directly over.

(*b*) Received 12 inspections, two of these being entrances.

(*c*) Received 40 inspections, none being entrances.

Experiment 7 differs from experiment 6 in no particular whatever except in the change which has rendered the blossom at (*a*) invisible, except from a certain position. The number of inspections at (*b*) and (*c*) remained practically constant for each half-hour period. It is interesting to note, however, that (*a*), receiving 48 inspections in experiment 6, received but a single inspection in experiment 7. A change in surroundings which makes a blossom less visible to the visual sense of bee visitors at once decreases the number of inspections.

Experiment No. 8.—July 27. Time of observations ten minutes from 11:38 to 11:48 A.M. Blossoms in the triangular arrangement, with no change whatever from the preceding experiment except in making the blossom

at (*a*) again as visible as in experiment 7 by pushing aside the surrounding leaves.

(*a*) Is inspected 15 times, including one entrance.

(*b*) Is inspected 7 times, including two entrances.

(*c*) Is inspected 13 times with no entrances.

The blossom at (*a*) has now become as attractive to the bees as those at (*b*) and (*c*) which serve as controls.

Experiment No. 9.—July 27. Period of observation 15 minutes, from 10:50 A.M. until 12:05 P.M. Triangular arrangement as in preceding experiments with the following changes:

(*a*) Petals of (*a*) in experiment 8 are removed and artificial crêpe paper petals of nearly the same color are substituted.

(*b*) Artificial blossoms growing *in situ* as a control.

(*c*) Artificial floral structure used at (*c*) in experiments 7 and 8.

(*a*) Receives only two inspections.

(*b*) Receives 16 inspections, including two entrances.

(*c*) Receives 3 inspections, including one entrance.

The artificial nature of the paper petals at (*a*) was at once perceived by the bees in their passing flights. The few inspections noted were indicated by a momentary pause in flight quite unlike the more prolonged hovering movements over the blossom at (*c*).

Experiment No. 10.—July 27. Period of observations 20 minutes, from 12:05 P.M. to 12:25 P.M. The same triangular arrangement was used as before. The only change from experiments 8 or 9 consisted in placing three real cotton petals carelessly upon the paper petals at (*a*) in such a way that only part of the paper petals was concealed. Blossoms (*b*) and (*c*) were left unchanged.

(*a*) Receives 11 inspections.

(*b*) Receives 7 inspections, including one entrance.

(*c*) Receives 21 inspections.

Passing bees were at once led to inspect the real petals placed at (*a*), although these very imperfectly covered the artificial paper petals beneath. No very decided re-

pellent odors can be held to reside in the artificial paper petals which failed to attract passing bees when used alone.

Experiment No. 11.—July 27. Observations for this experiment continued 10 minutes, from 1:26 to 1:36 P.M. The triangular arrangement was used.

At (*a*) a single real cotton-blossom petal is pinned to a stem.

At (*b*) a cotton bud and calyx simulated by neatly wrapping a portion of a cotton leaf around the base of five real petals rolled together.

At (*c*) a normal open cotton blossom growing in situ as a control.

DATA FOR EXPERIMENT NO. 11

Points of Triangle	Total Inspections	Distribution by Species				Total Entrances	Distribution by Species				
		Melissodes sp.	*Elis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Elis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	2	2										
(*b*)	8	8										
(*c*)	3	3										

The single petal at (*a*) is sufficient to invite the inspection of passing bees, although there is little more than a fraction remaining of the size and color of a normal open cotton blossom. The writer has observed that a partly opened bud, as represented at (*c*), appears to invite more frequent inspection and entrance than a fully expanded blossom which has been much oftener entered by bees. It is possible that bees in their entrances leave traces of odors which are detected by later visitors, causing them to pass on in search of fresher blossoms.

Experiment No. 12.—July 27. Period of observations one half hour, from 1:36 to 2:06 P.M. In this test, which practically duplicates experiment 11, two blossoms were used in the same row and on plants about three feet apart.

At (*a*) a single petal was pinned to a stem.

At (*b*) control. A normal cotton blossom *in situ* as grown.

The single petal at (*a*) received 16 inspections, some of which were very thorough, as a number of bees appeared to examine the petal intently from all sides. The control blossom at (*b*) received 26 inspections, including 8 entrances within. In both cases the visiting bees were all species of *Melissodes*.

Experiment No. 13.—July 27. Period of observations one half hour, beginning at 2:06 P.M. and ending at 2:36 P.M. Two blossoms were arranged in the same row as in the preceding experiment.

At (*a*) a perfect cotton blossom was pinned in the same relative position as the blossom at (*b*).

At (*b*) control. A perfect cotton blossom growing *in situ*.

The blossom at (*a*) received 7 inspections, including one entrance. The blossom at (*b*) received 12 inspections, including 5 entrances. Species of *Melissodes* were the only visitors.

Experiment No. 14.—July 28. Time of observations one half hour, from 9:15 to 9:45 A.M. Three blossoms were arranged on three consecutive plants in the same row. Throughout this series of experiments for July 28, these positions were unchanged. See the diagram.

At (*a*) control. A perfect cotton blossom pinned in position.

At (*b*) large blossom of a wild convolvulus (white with a deep purple throat) was pinned in position.

DATA FOR EXPERIMENT NO. 14

Points of Triangle	Total Inspections	Distribution by Species					Total Entrances	Distribution by Species				
		Melissodes sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	15	12				3	1					1
(*b*)	14	12				2	0					
(*c*)	14	11				3	0					

At (*c*) control. A perfect cotton blossom pinned in position.

Although strikingly unlike a cotton blossom in color and general appearance, the convolvulus blossom attracts attention quite as often. It is hardly to be expected that the bees would enter it as frequently as a cotton blossom, if at all, since it is a well-known habit of many bees to confine their visits pretty constantly at any one time to blossoms of the same species of plant. Especially has this been shown true for the honey bee by Hermann Müller and others. M. H. Mendleson, of California, affords an instance where a single colony out of 200 visited solely mustard flowers, while the rest gathered from sage blossoms alone.[2]

Experiment No. 15.—July 28. Time of observation one half hour, from 9:45 to 10:15 A.M. Blossoms arranged in the same row as before with the following changes:

At (*a*) petals removed from the blossoms of preceding experiment.

At (*b*) same white convolvulus blossom used in the preceding experiment.

At (*c*) control. Same cotton blossom of preceding experiment pinned in position.

DATA FOR EXPERIMENT NO. 15

Points of Triangle	Total Inspections	Distribution by Species					Total Entrances	Distribution by Species				
		Melissodes sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	0											
(*b*)	19	17				2	0					
(*c*)	20	20					0					

By the removal of the petals of a cotton blossom as at (*a*), the blossom no longer advertised itself to the attention of bees, as has been demonstrated in previous experiments. In the present test, although the white con-

[2] Mendleson, M. H., "Gleanings in Bee Culture," October, 1908, 36.

volvulus blossom had completely wilted and collapsed, its noticeable color alone continued to invite inspection by passing bees quite as often as the control blossoms at (*c*).

Experiment No. 16.—July 28. Period of observation one half hour, from 10:15 to 10:45 A.M. The three points in the preceding experiment were used as follows:

At (*a*) a single cotton petal was placed on the blossom of the preceding experiment, from which all the petals had been removed.

At (*b*) a single cotton petal was loosely pinned to a stem.

At (*c*) control. A normal cotton blossom pinned in a conspicuous position.

The blossom at (*a*) receives 8 inspections.

The petal at (*b*) receives 9 inspections.

The normal blossom at (*c*) receives 27 inspections with no entrances. All visitors were *Melissodes*, except a small bee which inspected (*c*).

As the blossom at (*c*) was conspicuous from all sides, the writer judged that this fact accounted for the much greater number of inspections given this blossom, since (*a*) and (*b*) were visible almost wholly from one side only. In the next experiment this question was further tested.

Experiment No. 17.—July 28. Period of observation one half hour, from 10:45 to 11:15 A.M. In this experiment the only changes from the preceding consisted in an interchange of material.

DATA FOR EXPERIMENT NO. 17

Points of Triangle	Total Inspections	Distribution by Species					Total Entrances	Distribution by Species				
		Melissodes sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	8	8					0					
(*b*)	22	21				1	0					
(*c*)	27	25				2	0					

At (*a*) single detached petal pinned to leaf stem.

At (*b*) control. Normal cotton blossom pinned in position.

At (*c*) the cotton blossom with its single replaced petal at (*a*) in preceding experiment.

In this experiment the more exposed position (*c*) appears to be of considerable advantage to a blossom located here, even though its normal appearance is greatly changed by mutilation. The general form and appearance of a cotton blossom, as a whole, does not appear to play a very important rôle in initiating the procedure of inspection by passing bees, since a single detached petal receives quite as many inspections as a normal blossom.

Experiment No. 18.—July 29. Observations continued one hour, from 8:20 to 9:20 A.M. In this experiment three blossoms were used, as in previous experiments, and arranged on consecutive plants in the same row. A blossom of an Asiatic cotton (*Hawasaki*) was compared with two ordinary American upland blossoms as controls.

(*a*) control. Normal American upland blossom pinned in position.

(*b*) *Hawasaki* blossom entire pinned in position.

(*c*) control. Normal American upland blossom pinned in position.

DATA FOR EXPERIMENT NO. 18

Points of Triangle	Total Inspections	Distribution by Species					Total Entrances	Distribution by Species				
		Melissodes sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	20	19		1			0					
(*b*)	14	12		1		1	0					
(*c*)	29	24		1	1	3	2				1	1

Experiment No. 19.—July 29. Observations continued one half hour, from 9:25 to 9:55 A.M.

(*a*) Control. Normal American upland blossom pinned in position.

(*b*) Control. Normal American upland blossom pinned in position.

(*c*) *Hawasaki* blossom entire (af *b*) in last experiment.

DATA FOR EXPERIMENT NO. 19

Position of Blossoms	Total Inspections	Distribution by Species					Total Entrances	Distribution by Species				
		Melissodes sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	11	8				3	0					
(*b*)	10	7			1	2	1				1	
(*c*)	3	2				1	0					

Experiment No. 20.—July 29. Observations continued one half hour, from 10:50 to 11:20 A.M.. Three blossoms arranged in the same row as for previous experiments.

(*a*) Control. Normal American upland blossom pinned in position.

(*b*) *Hawasaki* blossom entire at (*c*) in experiment 19.

(*c*) Control. Normal American upland blossom pinned in position.

DATA FOR EXPERIMENT NO. 20

Position of Blossom	Total Inspections	Distribution by Species					Total Entrances	Distribution by Species				
		Melissodes sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	20	8	1	1		10	3		1	1		1
(*b*)	10	8				2	0					
(*c*)	16	6		1	1	8	2	1				1

REPRODUCTION IN THE BROWN RAT (MUS NORWEGICUS)

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IN view of the fact that the brown rat is playing such an important rôle in the economic field and the medical world at the present time, it is of interest if not of practical value to know the details of its reproduction. The life history of this species as lived in its natural environment is as yet imperfectly known. It was to bridge this deficiency in our knowledge that data were obtained on a number of rats kept in the laboratory from November 5, 1909, to December 8, 1910. My results may be much different from those of natural conditions, yet I am convinced that the results obtained are not radically different from what actually takes place in nature where shelter is good and food abundant.

Two sets of cages of four each were built. The first consisted of revolving cages, a foot wide and eighteen inches in diameter with nesting boxes, measuring $8 \times 5 \times 5$ inches, suspended from the axles. These cages were similar to those used by Slonaker. The second set of cages were rectangular, measuring $24 \times 24 \times 8$ inches. These were made of screening, three wires to the inch. For the sake of cleanliness the cages were suspended, as shown in Fig. 1. Newspapers were spread

beneath all the cages to catch the excrement and removed as occasion demanded.

In all the cages, siphon watering troughs were used; *i. e.*, bottles held upright with their mouths dipping into shallow dishes. Open vessels were objectionable because rats drop their excrement as they climb about in the cage, thus polluting the water.

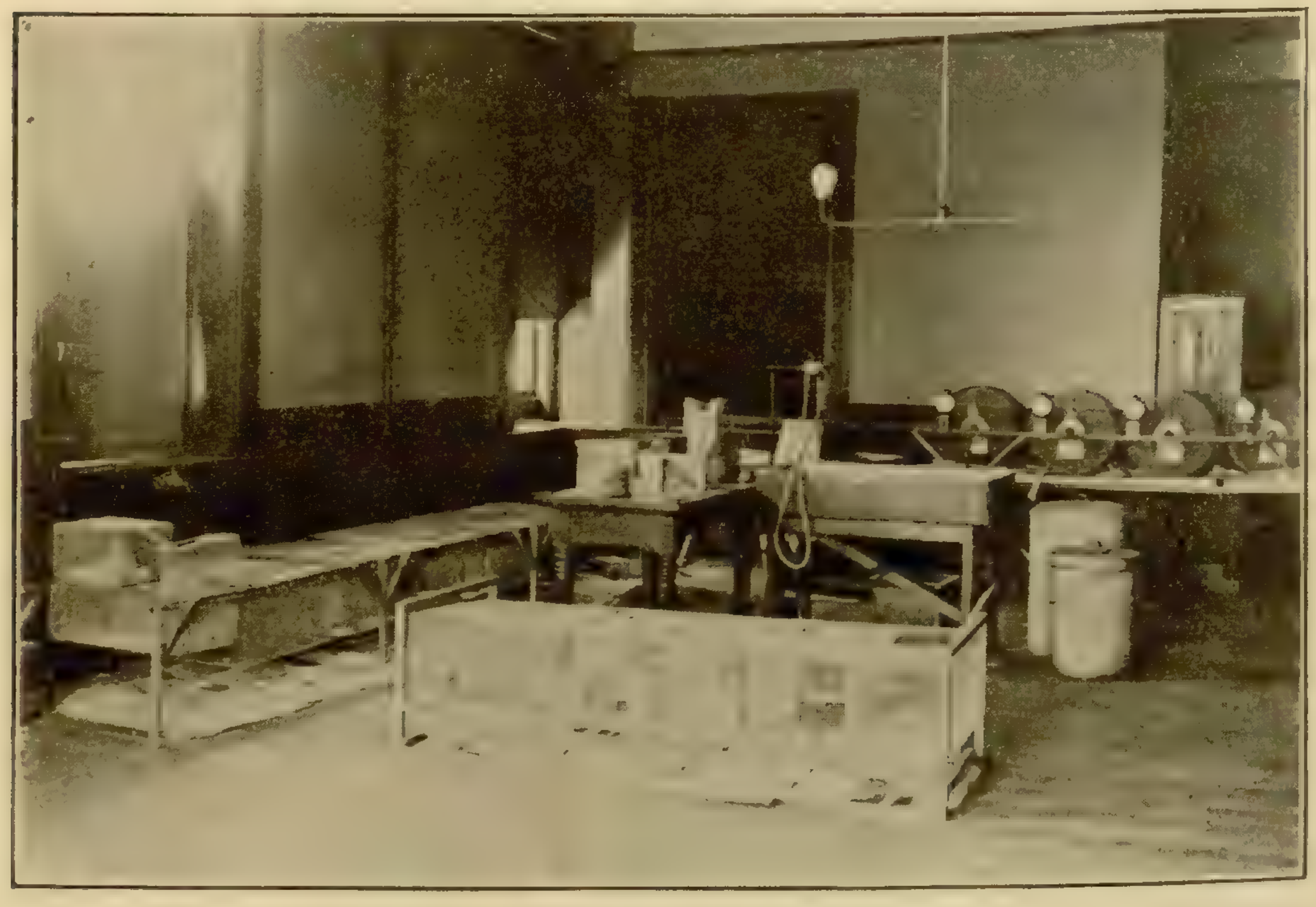

FIG. 1. Showing the plan of the cages.

The experiment was started November 5, 1909, with seven pairs of rats which had just been caught. For convenience, each pair was numbered, the first four being in the revolving cages and the other three in the stationary. The pairs numbered 1, 2 and 5 were old (adults), the females apparently having given birth to young. The others were probably in their third to sixth months and had not given birth.

Female No. 6, after giving birth to young on December 31, 1909, was severely injured by her mate. The wound was not yet healed September 12, 1910, when she was killed, at which time she was found pregnant. The following table is the reproductive record of the other six pairs.

REPRODUCTIVE RECORD. FIRST GENERATION

Date	No. of Pair	No. of Litter	No. of Young	Male	Female	
Feb. 4, 1910	1	1				All eaten February 5. Male not taken away.
Feb. 26, 1910	7	2				All dead-part eaten February 28. Male taken away February 26.
Feb. 27, 1910	1	3	11	5	6	Male taken away February 27.
Mch. 14, 1910	2	4				All dead July 21. Male not taken away.
Mch. 22, 1910	3	5				Male taken away March 22.
Mch. 22, 1910	4	6	7	4	3	
Apr. 7, 1910	7	7	12			All dead April 10.
May 4, 1910	7	8				All eaten May 9.
May 16, 1910	2	9				
May 22, 1910	3	10				
May 22, 1910	1	11	12	4	8	Male not removed.
June 1, 1910	7	12				All eaten June 3. Male removed before birth.
June 4, 1910	5	13				All eaten June 4. Male removed before birth.
June 30, 1910	7	14				All eaten July 6. Male removed before birth.
July 23, 1910	7	15				All dead July 24. Male removed before birth.
Aug. 24, 1910	4	16				All eaten August 27. Male not removed before birth.
Sept. 3, 1910	5	17				
Sept. 5, 1910	7	18	11	4	7	Male removed before birth.
Sept. 8, 1910	2	19	10			All dead September 29. Male removed before birth.
Sept. 20, 1910	1	20				Four still alive. Male removed before birth.
Sept. 20, 1910	3	21	10	6	4	Nine still alive. Male removed before birth.
Sept. 26, 1910	4	22				All eaten. Male removed before birth.
Sept. 26, 1910	5	23				All eaten. Male not removed before birth.
Oct. 17, 1910	2	24				All eaten. Male not removed before birth.
Oct. 20, 1910	5	25				All eaten. Male removed before birth.
Nov. 26, 1910	4	26				All eaten. Male removed before birth.
Nov. 26, 1910	7	27				Part eaten. Male removed before birth.

REPRODUCTIVE RECORD. SECOND GENERATION

Females of Litter No. 11

Date	No. of Female	No. of Litter	No. of Young	Male	Female	
Oct. 15, 1910.	11–2	28				All eaten. Male removed.
Oct. 17, 1910.	11–5	29				All eaten. Male removed.
Oct. 24, 1910.	11–6	30	9			Part eaten — others removed. Male removed.

The works of Lantz and Boelter lead us to infer that the brown rat breeds the whole year round. My rats gave birth to young from February to December, inclusive, and, since they were seen mating in November, De-

cember and January, it is safe to say that they produce young in January, also, which gives their breeding period as the whole year.

The gestation period was found to be $23\frac{1}{2}$ to $25\frac{1}{2}$ days, counting from the time of the first copulation. If $23\frac{1}{2}$ days is the shortest time, then females Nos. 1 and 7 must have mated on February 4 and June 30, respectively, the days they gave birth and also ate their young.

Frequently a female eats her young and when she does so, she may breed immediately. It is seen from the table that female No. 7, which had the habit of devouring her young, gave birth to seven litters at intervals of about thirty days; *i. e.*, taking February 2 as the date of conception for her first offspring, she produced, seven litters in seven months.

If the young are reared, a second litter may be produced in two months. Some do not give birth so soon, which may be due, largely to the fact that a female is not sure of conceiving at any given copulation. Daniel's experiment with white mice seems to have some bearing on this point. He found that a female suckling a large litter, carried the second longer, as much as ten days over the average gestation time. According to my data, the brown rat does not conceive before the last ten days of the lactation period, which should not have so marked an effect on the gestation period as is found in the case of the white mouse, which becomes pregnant as soon as a litter is born.

The number of young in the eight litters which I was able to count varied from seven to twelve, with an average of 10.5. Boelter quotes Brehm as recording a litter of twenty-one. Lantz gives two cases where seventeen embryos were found in one female and nineteen in another. He also thinks that for temperate regions the average litter is not under ten. From the data at hand, we can conclude that a pair of adult rats is capable of rearing fifty to sixty young per year. Zuschlag's theoretical table, as quoted by Boelter, gives sixty-four as

the possible number of young at the end of the year, the product of a single pair. In this table Zuschlag assumes eight to be the average number of young per litter, and eight litters per year to be the product of a single pair. On this basis the number of offspring at the end of the second and succeeding years is far in excess to the number computed on experimental data.

Rats begin mating, as a usual thing, about five o'clock P.M., and to obtain the period of gestation, males were placed with the females every day at this hour. If a female was in heat, she was removed to a separate cage with one to three males. At first females were left with the males not more than two hours, in which time many copulations had taken place, but in no case did a pregnancy result. Later, they were left with the males twelve to fifteen hours, and even then, failures to become pregnant far outnumbered the pregnancies.

I have not observed a single case of a female mating with a male smaller than herself. It is not common for an old female, even when in heat, to chase a young male about the cage as though he were a female, not letting him come near her. This same female, if placed with a larger male, which could boss her, would mate with him at once without any opposition. Mating in this case seems to be, to some extent, dependent upon the dominating ability of the male.

The number of coitions during a single period of heat is, apparently, great. In one case a female, placed with four males, mated with them in such rapid succession that fifty attempted coitions per half hour would be a conservative estimate. It is impossible to say how many of these attempts were successful, because the rat requires such a short time (four seconds being a long time) to perform the act, thereby making the details of the process difficult of observation.

The following table is a month's record of seven females kept to determine the frequency of the mating periods. Such periods are indicated by an X. It is

FEMALE

Date	October															November																	
	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
No. 11-1																									×								
Wild									×										Pregnant														
No. 11-4								×											×										Non-preg.				×
No. 11-2										×				×						×									×	Non-preg.			
No. 8									×											×					×					×	Non-preg.		
No. 7	×							×									×				Pregnant												
No. 4								×										×					Pregnant										

seen that only one pregnancy occurred as a result of each six times of mating. The table indicates, also, either that the mating periods come irregularly, or that the females come in heat about every five days.

I am convinced that odor is the final test for sex recognition. When rats are placed together, the males assume an aggressive attitude and fight all those that oppose them. The females may, usually do, for a little while, resist the males; but they soon yield. They then lie on their backs entirely passive, while the males nose them about the head and smell of their genital organs. This attitude is frequently taken by pregnant females. The males in such cases have shown their superiority and the females recognize it. From now on there is little fighting on the part of the males, and afterwards they will often permit themselves to be severely punished by the females without injuring them. Copulation does not usually follow the above proceedings.

When males meet, there is a battle royal until one is recognized victor. The conquered, then, tries to elude the stronger, and will not submit to be smelt of as a female. Often males smell of each other, probably determining one another's sex, before beginning the fight. I am sure there is no sex recognition when the fight is begun at once, for the females are treated in the same way.

There is very little courtship among the rats. The male is absolutely silent and the female almost so during the period of heat. A pair which had been together for several months, were seen to arouse from their sleep at five-thirty o'clock, P.M., and begin copulating at once without any preliminaries at all. They had not mated previously during the day.

When a female resists the advances of the male, she does so by fighting him away, as shown in Fig. 2, or by kicking him away with her hind foot; or she may lie on her back, as previously described. On the other hand, a female in full heat is the more active of the two. In one

instance, she was seen to clasp the male. If he is not aggressive, she throws herself before him in a crouching position, a procedure which she repeats until he takes notice of her. Again, she may strike his head, as though fighting, until he follows her. A female in full heat is much more active and less pugnacious than at other times.

FIG. 2. Rats in a fighting attitude.

We find the anomaly of mammals eating their young carried to an extreme in the case of brown rats kept in confinement. My records show a large per cent. eaten, almost fifty, which has much to do with the number of litters per year, consequently the number of young. This infanticide has usually been attributed to the male, but the young are eaten whether the male is or is not

present at the time they are born, which throws the blame on the female. In fact, I have no direct evidence against the male.

The young, when eaten, may be devoured at birth or any time within the next four days. It has been suggested—I think with a little basis for the statement—that disturbing the parents causes them to eat their young. W. T. Hornaday, in a letter, and Bostock state that the large carnivora are kept from all disturbing influences at and about the time they are giving birth. In rare cases some species devour their young if disturbed, but more frequently the young are deserted. My rats were in a room which was kept locked and free from any disturbing influences except my morning visits. Frequently, females by themselves, which built their nests in closed boxes, have had their young and eaten them between my visits. In such cases these females could not have been disturbed. On the other hand, I have taken the young from the nests, weighed them, and even handled them without the mother injuring them when replaced.

Another suggestion is that the rats have not had enough flesh diet and, when the young are born, eat them to satisfy their desire for meat. Here again I think there is no truth, provided plenty of grain and vegetables are accessible. My rats have eaten their young when on a meat-grain-vegetable diet, as well as when on a grain-vegetable allowance.

Dr. Slonaker suggests that the same motive, which leads the rats to eat their dead under natural conditions, might also cause them to eat their helpless young. This is in accord with the rat's habit of killing off its weak.

One of the reasons for eating the young, I think, might be found in the habit that mammals have of thoroughly licking their young, and in many cases eating the embryonic membranes, even among the herbivorous animals. It seems but a little step from the eating of the placenta to the devouring of the young. There may be some

truth in all these theories, but I doubt if the principal cause has yet been suggested.

CARE OF THE YOUNG

Before the young are born, the female builds a nest as elaborate as the means at hand will permit. Almost any sheltered nook about buildings is a suitable nesting place for the brown rat. On the farm, in addition to breeding about buildings, it digs its burrows in the field and nests in old straw stacks and grain still in the shock. The nest consists for the most part of a coarse substance such as straw or corn husks, with a lining of a softer material, especially feathers when obtainable. Blue found that where rats use run-ways, they nest in a branch leading off from the main course. This branch is in the form of a Y with the nest in one arm and a storehouse in the other.

The young at birth are entirely helpless. The mother gets them all together and then huddles over them for hours at a time. She never lies on her side to let the young suck; she always crouches over them while the young lie on their sides or backs to get hold of the teats. Usually all the young nurse at the same time, and a litter of twelve, at about weaning time, almost holds the female off her feet while they suck.

The female can easily be induced to move her young elsewhere by disturbing the nest. The young only a few days old are caught around the body by the mother, but if they are a week or so old, she takes hold of them by the skin. In the latter case they are carried much as a kitten is carried by its mother.

In the laboratory the female spends most of her time with the young; some even carry all their food into the nests. Taking food into the nest is a common habit of the rat and must not be considered as a trait peculiar to females with young.

GROWTH

The young at birth weigh on an average 6.4 grams. The males are a little the larger, measuring in body

length 52 mm. as compared with 49 mm. for the females. They also weigh more, and by the end of the second week are as much as two grams heavier.

Very little change is noted in the appearance of the young the first two days, save a gain in size and strength. On the third day a change in color can be detected. The flesh tint is being replaced by a darker hue with a decided tinge of blue on the distal portion of the tail. Curiously enough, the tail is the first to show any marked change of color. On the fourth day, the tail is still darker and the flesh color of the dorsal parts has been replaced by a gray with a touch of blue. Up to this time, no hair is noticed except the vibrissæ. By the end of the week the body is covered with a thin coat of very fine hair, which gives a delicate bluish-brown color. The coloring of the legs begin about this time with the palms of the feet, the joints of the toes and legs turning a bluish tint. The tail, in the meantime, has darkened almost to the base and the nose turned nearly black. On the eighth or ninth day, the gray of the adult is noticed on the back of the head and neck, and with this as a center, it spreads until about the eighteenth day, when the whole color is that of the adult with the exception that it is darker and softer.

The following is a diary of litter No. 18 for the first twenty-five days. The weights given are the averages for the whole litter.

Day	Wt. Grams	Notes
1	6.1	Flesh color; blind; ears closed; helpless.
2	6.4	Able to right themselves if turned over.
3	7.2	Color changing to bluish tint on the dorsal parts; tail coloring from the distal end; no hair except vibrissæ.
4	8.1	Flesh color limited to the ventral parts; creeping about in the nest.
5	9.0	Color a bluish-brown on the back and sides.
6	9.8	
7	10.7	
8	11.5	Sparsely covered with short fine hair.
9	12.3	Faint brownish tinge on the back of the head and neck; tail a dull blue except about 4 mm. at its base; joints of the feet and legs, also the palms of the hind feet, blue; under parts, pinkish.

10	13.0	Dorsal parts, a delicate brown; nose, almost black; incisors appear in the upper jaw.
11	13.8	Heels almost black; rest of coloring the same as yesterday; one seen sitting up and washing its face.
12	14.8	Lower incisors appear (all the incisors appear on the same day in some cases; usually the lower appear a day later than upper).
13	15.1	All the dorsal parts are brown.
14	16.0	
15	16.9	
16	17.9	Eyes beginning to open; one young attempted to bite me.
17	18.8	All have their eyes open; color the same as that of the adults except that it is darker and softer.
18	19.8	
19	20.2	
20	21.0	
21	20.9	Found the young hungry and when given a dog-biscuit, they ate it greedily. It is probable that they began taking solid food the first or second day after cutting their lower incisors, and judging from their weights, yesterday was the first day they did not have food they could eat.
22	23.0	
23	23.9	
24	24.9	
25	25.9	From now on there is little change noticed except increase in size. The young have grown rapidly from the first without the initial loss of weight as found in human infants, or even a marked retardation as found in guinea-pigs by Minot.

During the sixth week the young are weaned. At this time they weigh fifty to seventy grams, and are able to take care of themselves, provided food is abundant. I have seen a number of rats of about this age and size wandering about, in or around farm buildings, apparently, in a starved condition. Presumably, these had just been weaned and were unable to find suitable food.

If food has been abundant the males, by the end of the sixth month, weigh 230 to 290 grams while the females weigh 170 to 240 grams. The male and female of one of my pairs, kept throughout the year and which I judged to be in their third month when caught, weigh 337 grams and 223 grams, respectively. My old male No. 5 weighs 460 grams and my oldest female, 345 grams. These data indicate that a rat does not reach its full growth before the end of the eighteenth month.

Sexual maturity is attained much sooner than full growth. One female of litter No. 11 conceived on the day she was four months old, hence giving birth to her first young in her fifth month. The males are sexually mature as soon as the females, and I have seen some indications that they may be mature early in their fourth month.

Conclusions

1. The brown rat breeds in every month of the year.
2. The gestation period is $23\frac{1}{2}$ to $25\frac{1}{2}$ days.
3. The number of young per litter varies from six to nineteeen with an average of between ten and eleven.
4. Five or six litters may be reared by a single pair in a year.
5. Seven litters were born in seven months by one female and, presumably, twelve would be produced in the course of a year when all the young perish at birth.
6. There is very little courtship among the brown rats.
7. Odor is the primary factor in sex recognition; the aggressiveness of the male is second.
8. Brown rats in captivity eat almost fifty per cent. of their young at birth. Most of the young eaten, if not all, are eaten by the females.
9. Full growth is attained not under eighteen months.
10. Sexual maturity is reached at least by the end of the fourth month in both sexes.

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SHORTER ARTICLES AND DISCUSSION

DATA, DIALECTICS AND OTHER DIGRESSIONS

Some . . . persons vainly seek by dialectics and far-fetched arguments, either to upset or establish things that are only to be founded on anatomical demonstration, and believed on the evidence of the senses. He who truly desires to be informed of the question in hand, and whether the facts alleged be sensible, visible, or not, must be held bound either to look for himself or to take on trust the conclusions to which they have come who have looked; and indeed there is no higher method of attaining to assurance and certainty.—William Harvey, *Second Disquisition to John Riolon, Jun.*

To the Editor of the American Naturalist:

My reasons for asking you to publish the above from your September, 1911, issue are two: the text is excellent; the sermon is wide of the mark.

The text, the reader will have noted, heads a latest contribution to our knowledge of egg production in the domestic fowl[1] which Dr. Pearl has been prevailed upon to write up by the conviction that certain criticisms[2] "rest on either a misconception of what our results really are, or else a lack of understanding of the real facts regarding certain of the biological points involved." For his "endeavor, if possible, to remedy this defect in some degree at least" those biologists who are thereby instructed in matters of fact will doubtless be grateful.

The obvious implication of Dr. Pearl's quotation from Harvey and of his concluding remarks is that my arguments concerning the genotype concept are of a purely scholastic and "far-fetched" order.

In consideration of these implications and in justice to my paper which appeared in your June number may I call your readers' attention to the following points?

First. I certainly did not ". . . seek by dialectics and far-fetched arguments, . . . to upset . . . things that are only to

[1] Pearl, R., "Biometric Arguments regarding the Genotype Concept," Amer. Nat., Vol. 45, pp. 561–566, 1911.

[2] Harris, J. Arthur, "The Biometric Proof of the Pure Line Theory," Amer. Nat., Vol. 45, pp. 346–363, 1911.

be . . . believed on the evidence of the senses.'' Unfortunately for Pearl's excellent-in-itself quotation, the genotype theory is not a pickled specimen concerning the structure of which all the anatomists who can crowd around the table will agree. Quite to the contrary, it is a far-reaching generalization of the kind which should not be accepted until it has been shown not only to describe and epitomize the results of great series of actually observed facts but to stand every test which can reasonably be applied to it. A careful examination of all the pure line literature known to me had convinced me that in the enthusiasm for the new theory the elementary principles of scientific reasoning were often ignored and matters of plain common sense overlooked. I had frequently found biologists enthusiastically supporting the popular theory without knowing what its essential implications are. It seemed useful, therefore, to ''state the fundamental problems of the pure line theory as they appear to the biometrician'' and to call attention to some of the weak points in arguments in its support. Judging from some of the vagaries encountered in the genotypic literature since then, I fear that my plea for more caution, less assumption and less reasoning in circles in our theorizing about ''sensible, visible'' facts was rather wasted effort.

Second. My paper was written *before* Pearl's preliminary publication of the results of individual pedigrees in the same number of the AMERICAN NATURALIST, and before his advance statements concerning correlation in the paper just issued. If new and pertinent facts prove that my views were wrong the views will be discarded. When Dr. Pearl has given us all the data and not adumbrations merely—when all the cards are down, face up on the table—it will be time for a critic to show reasons for differences of opinion or to admit that he was wrong. Until that time it seems foolish—in fact dangerously near dialectics—to squander in argument space that might be used to publish tables of data. In passing, I must remind the reader that our present sore need is not *possible illustrations* of the genotype theory if valid but *critical evidence*[3] for or against it.

[3] Very unfortunately Pearl's sentence, ''So far as concerns . . . his personal opinion of the critical value of the work done in this laboratory no discussion will be entered upon by the present writer'' cuts two ways. Some of those who have not read what I really said will conclude that

Third. Insinuations concerning dialectics may perhaps justify a digression concerning data. During the past five or six years some 100,000 countings, weighings, measurements, etc., bearing directly on the problem of pure lines in garden beans—the species on which Johannsen based his studies—have accumulated in my notes. These data have taught me how idle it is to discuss the pure line problem without the most refined biometric analysis of large masses of data. Such analysis necessarily proceeds with disheartening slowness. But I have been able to see no advantage in dragging this material through a long series of preliminary papers necessarily based upon uncompleted work. When the data are all in, and arranged in an orderly manner they will be honestly set forth as "an accumulation of plain, unadorned facts, available to any one's inspection."

J. ARTHUR HARRIS.

COLD SPRING HARBOR,
September 15, 1911.

actually or tacitly—and quite unfairly—I drew in question the accuracy or trustworthiness of the observations. Others will do Dr. Pearl the injustice of thinking that if a criticism was made there was probably some justification for it. Both will be quite wrong. In five different places I drew attention to the importance of the work of Pearl and Surface and emphatically stated that our differences—which as yet I see no reason to cancel out—are merely those of interpretation. What I actually said was, "The work of Pearl and Surface with poultry and maize seems to me to have no critical bearing on the pure line problem." *Critical bearing* which I wrote seems to me to convey a meaning quite different from *critical value* which Dr. Pearl writes. A judge might recognize the critical value of an expert's observations and yet fail to see that his testimony had any *critical bearing* in a case.

NOTES AND LITERATURE

DARWINISM AND HUMAN LIFE

Professor James Arthur Thomson's recent[1] book under the title of "Darwinism and Human Life" is most attractive reading. Professor Thomson thinks independently and writes fascinatingly. He gives even the most familiar of subjects new color and atmosphere.

The matter of the book was given in 1909 as the "South African Lectures," whose "chief aim was to explain the gist of Darwinism." An endeavor was made to add to the necessarily general and somewhat familiar content of the lectures, suggestions of how "Darwinism touches every-day life, in farm and garden, in city and empire."

The Darwinian reader interested by this prospect of finding his old wine put into new bottles runs rapidly through the chapters with the familiar headings of What we owe to Darwin, The Web of Life, The Struggle for Existence, The Raw Materials of Progress, Facts of Inheritance and Selection: Organic and Social, nosing for Darwinism and Human Life. And he finds himself rather disappointed at first, for he does not discover as much of the practical interlocking of Darwinism and human affairs as perhaps he felt justified in expecting. But in the last chapter he does find it more obviously and in more abundance than elsewhere and he begins really to read. And lo, when he stops reading he finds that he has read the book, all of it, backwards! And is very glad he has. At any rate, all this is what I did.

Professor Thomson is a good selectionist; though not a bad one; that is, not one who has an all other possible evolution factors—phobia. However, Darwinism for him rests on, or is, mostly selection. And it is the possible play of selection in human life, its play among individuals, among societies and among races, on which most of his direct application of evolution knowledge to human affair rests. Hence organic selection, social selection, eugenics, selection of Utopias, reversed human

[1] Thomson, J. A., "Darwinism and Human Life," 245 pp., frontispiece (Charles Darwin), 1910, H. Holt & Co., New York.

selection, and the like, are the subjects of his more concrete "Darwinism and Human Life" paragraphs. But Professor Thomson recognizes the broader aspect of his subject. He sees that all of Darwinism, in its very broadest sense, has interrelation with all of human doing and becoming. And it is this recognition, and the constant suggestion of it, everywhere in his discussion of the familiar subjects of the "gist of Darwinism," that make even the practised Darwinian reader read with fresh interest the whole of the book; even if he does happen, as your reviewer did, to do it backward!

V. L. K.

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THE ORIGIN OF SPECIES IN NATURE[1]

DR. HENRI HUS

MISSOURI BOTANICAL GARDEN

UNIVERSITY OF MICHIGAN

AMONG the duties of the botanist is that of adding to the number of known species, varieties and forms. To reach this end several ways are open. One may, by studying the flora of new or insufficiently explored areas, not only extend the range of species formerly known, but add new species. The work of Setchell and his students, especially Gardner, done on the algal flora of the Pacific Coast, yields an excellent illustration.[2]

Sometimes it is possible to correlate with such investigations work of economic value. The results obtained by agricultural explorers working under the auspices of the Office of Foreign Seed and Plant Introduction of the Bureau of Plant Industry, U. S. Dept. of Agriculture and other[3] institutions, offer a case in point. Such work, to lead to the desired result, requires men of especial fitness, physical, moral and mental. Not only must they possess physical endurance to overcome the hardships with which they necessarily meet. Moral courage, moral strength are necessary to extricate them from the many

[1] Read, through the courtesy of Mr. Henry W. Anderson, before the Academy of Science of St. Louis, May 15, 1911. Contributions from the Botanical Laboratory of the University of Michigan, No. 125.

[2] Univ. Calif. Publ. Bot., 1[a] et seq., 1903–1910.

[3] Hansen, N. E., "The Wild Alfalfas and Clovers of Siberia, with a Perspective View of the Alfalfas of the World," Bull. No. 150, B. P. I., U. S. D. A., 1909.

Aaronsohn, A., "Agricultural and Botanical Explorations in Palestine," Bull. No. 180, B. P. I., U. S. D. A., 1910.

difficult positions in which they are bound to find themselves and to bring to a successful end the undertaking upon which they have embarked. Further, a thorough knowledge and an excellent judgment are essential. Yet none of these are sufficient unless they be complemented by an all-pervading love for the subject, a devotion which counts all obstacles as naught and persists in the face of difficulties which to most men would appear unsurmountable. Frank Meyer, agricultural explorer, now, for the second time, exploring eastern Asia—last heard of when entering Thibet—exemplifies this ideal. Such are the men who on their return to the civilized world bring back with them the rare plants which delight the collector and which, in themselves frequently of apparent insignificance, in a few years add immensely to our collections. The discovery of *Nicotiana Forgetiana*[4] is, in recent years, perhaps the most widely known instance through the part played by this species in the introduction to our gardens of *Nicotiana Sanderæ* (*N. alata* × *Forgetiana*). But not always is it necessary to draw on the flora of distant countries. By thoroughly going over a well-covered territory one may be able to add new varieties of a more or less well-known species, such as was the case with *Oxalis stricta viridiflora*,[5] which, since the time of publication of the original paper, has been found near Thomson, Ga.[6] This plant, since the spring of 1909, has established itself in the Ann Arbor experiment garden, spreading rapidly from seed selfsown in the latter part of the same summer. The plants grow in the open as well as in more shaded places and on a light, sandy soil. The varietal character maintains itself perfectly, as it does in the Missouri Botanical Garden, where, on a recent visit, I saw a bed of it, in the open and on a fairly heavy soil. Though there is a certain amount of variation in the intensity of the green coloring of the

[4] *Curtis' Botanical Magazine*, 4th Ser., **1**, pl. 8006, 1905.

[5] Hus, H., "Virescence of *Oxalis stricta*," Ann. Rep. Missouri Bot. Gard., **18**: 99, pl. 10, 11, 1907.

[6] Bartlett, H. H., "On *Oxalis stricta viridiflora*," *Rhodora*, **11**: 118, June, 1909.

flower, due to a variation in the relative amounts of chloroplasts and yellow chromoplasts, the plant appears to have undergone a sufficient number of fairly rigid tests, under widely divergent conditions, and for a sufficient number of generations (9), to entitle it to recognition as a distinct, non-pathological variety. The variation in the color of the flower I am inclined to ascribe to differences in light intensity. In a bed, situated in the middle of the experiment garden, *i. e.*, in an open place where no obstruction prevents full and direct illumination, the flowers are uniformly green. When the plants are grown in the greenhouse or in the shade of shrubs, there seems to be a tendency for the flowers to assume a more yellow tinge. But not in a single instance has a flower been observed which possibly could have been mistaken for one of the species.

Again it may be that a form deserving specific rank is discovered, as instanced by the now well-known *Capsella Heegeri*.[7] Such discoveries possess an added charm since in these cases the possibility of a recent origin of the new form is not excluded. Sometimes it is possible to prove this experimentally, as was done by de Vries for his evening primroses. An illustration of probably recent origin and of repetition of mutation is yielded by the discovery of a single specimen of the *inermis* variety of *Cynara Cardunculus* in Algiers by Trabut.[8] But some years ago what would seem to have been the same variety was grown in the St. Louis experiment garden from seed which my father kindly obtained for me from the then director of the Botanical Garden at Buenos Aires and the ancestry of which I understand was to be traced to an individual growing wild in the vicinity.[9]

[7] Solms-Laubach, H. zu, "Cruciferenstudien—I, *Capsella heegeri*, eine neuentstandene Form der deutschen Flora," *Bot. Zeit.*, **55**: 167, pl. 7, 1900.

[8] Trabut, L., "Sur une mutation inerme du *Cynara Cardunculus*," *Bull. Soc. Bot. Fr.*, **57**: 350, 1910.

[9] *Cynara Cardunculus*, a native of the Mediterranean region, emigrated to South America, where it occupies large areas (Darwin, "Animals and Plants under Domestication"). An analogous case is that of *Silybum Marianum*, likewise a native of the Mediterranean region and now largely

Generally speaking, the investigation of the flora of a newly discovered or formerly inaccessible region is a matter of choice or, better, perhaps, opportunity. The same is true for the detailed study of our collective species, leading to a recognition of component elements as illustrated by the work of Small on *Oxalis*,[10] *Rhus*, etc. Whoever can devote a part of his time to the study of a genus is able to establish the existence of differences which, formerly ignored and in themselves slight, are of the greatest importance for the tracing of relationships. Unfortunately, perhaps, in such studies there is usually developed a mass of detail so great, so intricate that none but a few specialists are able to recognize the various forms. *Hieracium, Aster, Cyperus* are names sufficient to strike terror in the hearts of any but the most ardent systematists. But before such a detailed study can be made there must be gathered, in the first place, herbarium material. It is not sufficient to possess a single specimen. Material must be collected from various habitats and both during the flowering and fruiting periods. Often there are differences between the leaves of old and young shoots, as in *Cratægus*. Or the leaves of the fruiting branches may be different from those of purely vegetative shoots as in *Hedera Helix*. *Ficus* and *Pothos* both may show leaves of a very different character.[11] None would at first sight believe leaves of seedlings or of adventitious shoots of *Eucalyptus globulus* and those of older specimens to belong to the same species. Many species of *Acacia* show, during the first few years of their existence, well-developed phyllodes which later disappear entirely. Sometimes even the leaves on the same

naturalized in California where it forms a common and, on account of its leaves, a most conspicuous weed.

[10] "North American Flora," **25**[1]: 25, 1907.

[11] In the greenhouses of the Missouri Botanical Garden may be seen a very fine specimen of *Ficus repens* which near the ground and up to a height of some eight feet, produces the small leaves typical of this species. When, however, the plant makes a bend to twine horizontally along a rod, large leaves are produced. Other instances are given in de Vries's "Species and Varieties," Ch. 15.

shoot may present a very different appearance. And while this is something not entirely unexpected in hybrids as in *Quercus Leana* (*Q. coccinea*×*imbricaria*) and Boston fern hybrids, it is a source of astonishment when this occurs in species which we do not believe to be of hybrid origin. Heterophylly is a matter of common observation in the ubiquitous horseradish, *Radicula Armoracia*. *Sterculia diversifolia*, commonly cultivated in greenhouses, has leaves which are mostly ovate to lanceolate in outline and which are often entire or variously three- to five-lobed on the same shoot. The sassafras, *S. variifolium*, illustrates the same principle, in fact, derives its name from this feature. The paper mulberry, *Broussonetia papyrifera*, shares the irregular lobing of the leaf with its near relatives, *Morus rubra* and *M. alba*.[12] The cut-leaved Persian lilac is very variable in this respect.[13] Sometimes seasonal differences are so great as to make collecting throughout the year an absolute necessity,[14] an instance so strikingly illustrated by *Viola palmata*. In woody plants there is not infrequently a return to the nepionic stage in the leaves produced near the base.[15] When we remember that heterochromatism[16] may add a further complication, it becomes evident that it is not sufficient to be able to refer to herbarium specimens only. The living plant must be studied in its various stages of development. It is by this means only that one may arrive at a true estimate of the stability and significance of minute details.

[12] Rep. Bot. Dep. New Jersey Agric. Coll. Exp. St., 325, pl. 21, 1909. Fry, A., "Note on Variation in Leaves of Mulberry Trees," *Biometrica*, **1**: 258, 1902.

[13] Masters, M. T., "Vegetable Teratology," fig. 177. See also, Schlechtendal, *Bot. Zeit.*, **13**: 559, 1855, and Lloyd, *Torreya*, **2**: 137, 1902.

[14] Cushman, J. A., "Studies of Localized Stages of Growth in some Common New England Plants," AM. NAT., **36**: 865; *ibid.*, **37**: 243, **38**: 819.

[15] Jackson, R. T., "Localized Stages in Development in Plants and Animals," *Mem. Boston Soc. Nat. Hist.*, **5**: 89, 1899.

[16] Kerner von Marilaun, A., "The Natural History of Plants," **1**: 149; **2**: 569.

Trelease,[17] in a recent paper on his favorite agaves, says: " . . . my own conception of specific identities and differences in the genus oscillates as my study proceeds. . . ."

While ultimately work of this nature, conscientiously carried out, leads to a clear delineation of the characters peculiar to each species, subspecies, variety, etc., there is reached, usually not so very long after the inception of the work and very long before its termination, a period of chaos which, to say the least, is the reverse of stimulating and ordinarily sufficient to dampen the ardor of the greatest enthusiast. Thus, in my cultures of local forms of *Capsella Bursa-pastoris,* the four forms described by Shull[18] and some of those of Almquist[19] can be recognized readily. But there remain so many whose classification is doubtful at the present time that it would cause Mr. Murdock, associated with me in this investigation, and myself to throw up our hands in despair, were it not for the fact that there have appeared in our cultures extreme forms, so striking and so different from any previously described, that we are inclined to believe we are possibly dealing with mutations in the sense of de Vries (Fig. 1). Research along these lines requires long and tedious experimental efforts. It is a different matter where the finding of distinctly new forms in an old territory is concerned. Here an element of chance largely enters. By increasing the number of our observations our chances of discovering something new may be increased materially. In other words, directly or vicariously a large amount of ground has to be covered. Yet I am not satisfied that a thorough knowledge of a comparatively small area would not lead to equally satisfactory results. The one requires about as much exertion as does the other and certainly the

[17] Trelease, W., "Species in *Agave*," *Proc. Amer. Phil. Soc.*, **49**: 232, pl. 32, 33, 1910.

[18] Shull, G. H., "*Bursa Bursa-pastoris* and *Bursa Heegeri* Biotypes and Hybrids," Carn. Inst. Publ., No. 112, 1909.

[19] Almquist, E., "Studien ueber die *Capsella Bursa-pastoris* (L.)," *Acta Horti Berg.*, **4**, No. 6, 1907.

number of observations is identical. But the greater familiarity with the territory and the fact that observation may be continued throughout the seasons offers certain advantages. It is a question which must be decided for individual cases by every investigator along this line,

Fig. 1. Appearance of a new form among seedlings of *Capsella Bursa-pastoris*. × 1.

since its answer must depend on local conditions, such as proximity to residence, climate, whether arid or temperate, etc. A garden, for instance, offers as good if not better opportunities to observe the appearance of new forms as does the field. Here all the requirements for such work are met with, *i. e.*, large numbers grown under highly favorable conditions. Parks, nurseries and especially the larger botanical gardens, where are kept accu-

rate records of the histories of the various plants grown, constitute an important field. Thus, in the Missouri Botanical Garden, there are grown every year numerous plants of *Bellis perennis* "delicata." In 1906 the seed for these specimens was obtained from a Philadelphia seed firm. The seed was sown and the plants were handled in the usual manner until they finally found their way to the beds used for decorative purposes. It was while the plants, several thousands in number, were in this position, that the attention of Mr. Shelby Jones, at that time a student at the garden, was attracted to a plant because of the abnormal character of its flowers. In the capitula of this specimen the rayflowers had either disappeared, or, what is more probable, had been replaced by

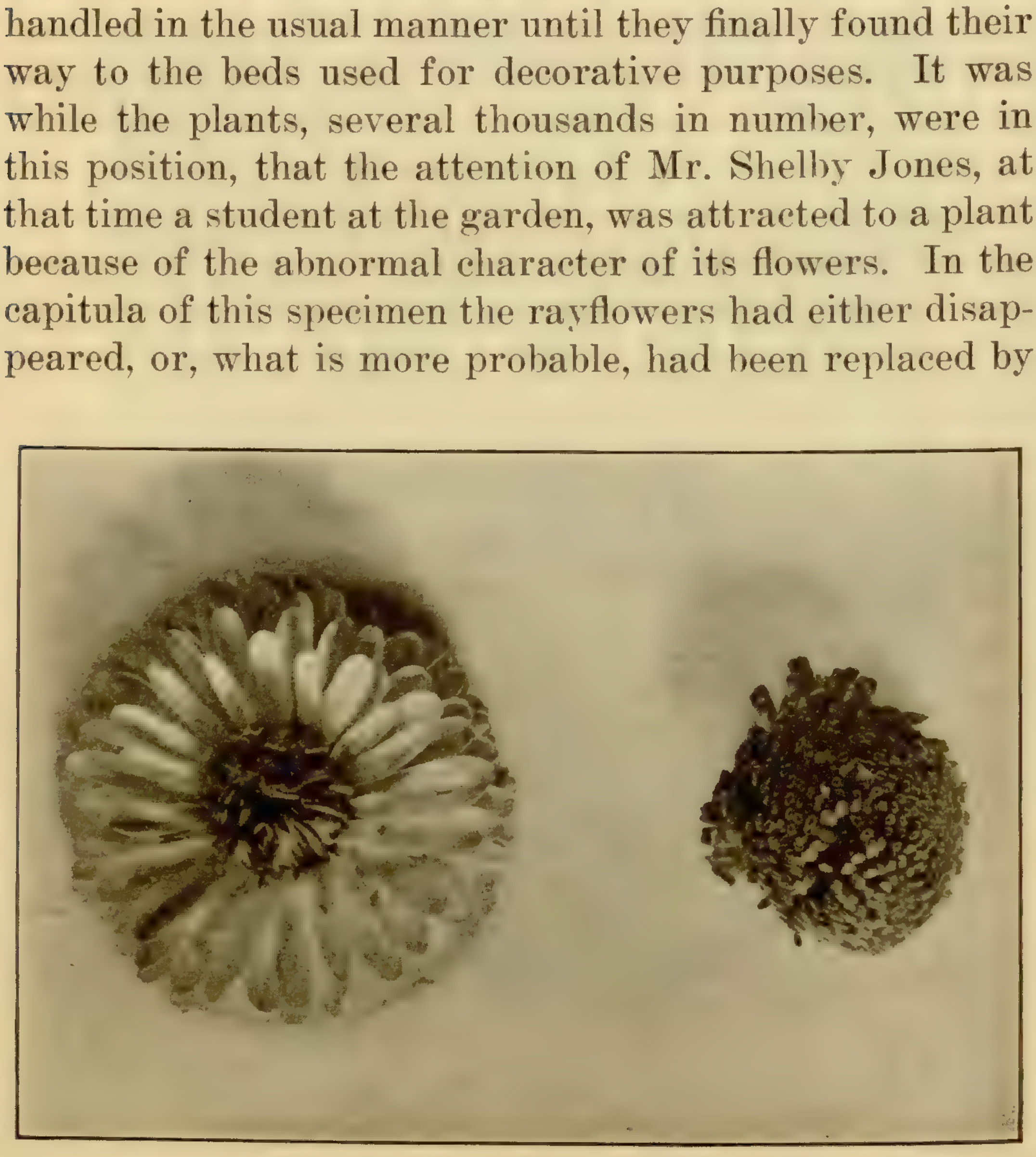


FIG. 2. Capitula of *Bellis perennis* "Delicata" and *Bellis perennis discoidea.* × 2.

disc-flowers. The result was a rather striking, maroon-red button, in sharp contrast with the normal heads (Fig. 2). For in the normal form of the variety under cultivation the upper surface of the ligules was either white or rose-colored, while the lower surface was red. In the discoid variety, owing to the tubular nature of the transformed

rayflowers, the white coloring disappeared from view. It is an instance of change of color analogous to that of the cactus dahlia, though differing in one striking feature. For in the latter case the brilliancy of the flowers is due to the recurved rayflorets which show the bright color of the upper surface instead of the dull shade of the lower one, exposed to view in the older form of dahlia.

The plant was segregated and propagated vegetatively, as many as one hundred specimens being on hand at a time. Among these not a single instance of a return to the conventional form was observed. Of course, it would have been far more interesting to note the result of sexual propagation, a proceeding which was rendered impossible by the failure of the flowers to produce good seed. This, however, is quite in accordance with the experience of horticulturists, *fide* André.[20] In this most comprehensive publication the variety *discoidea* is mentioned under the name of "Paquerette vivace var. double a fleurs tuyautées," its slight fertility noted and attention called to the fact that the seed for such plants must be collected from flowers which are almost double. It is added: "leur tendance a doubler est assez bien fixée pour qu'on ne trouve dans le semis presque plus de fleurs de duplicature imparfaite." In this connection Master's notes published in the appendix to his "Vegetable Teratology," and de Vries's remarks on *Matthiola incana fl. pl.*[21] are of considerable interest. Penzig evidently refers to a similar form,[22] though his use of the term "ox-eye daisy" for this form appears to be contrary to usage, it being reserved ordinarily for *Chrysanthemum Leucanthemum*. Similar instances are not rare among Compositæ and are illustrated by *Matricaria* (*Chamomilla*) *discoidea* and *Anthemis tinctoria discoidea*. Very frequently one is able to find a few tubular flowers among the rayflowers of our cultivated com-

[20] Vilmorin-Andrieux et Cie, "Les fleurs de pleine terre," 5th ed., R.-Ed. André, éditeur, 781, Paris, 1909.

[21] De Vries, H., "Plantbreeding," 238, Chicago, 1907.

[22] Penzig, O., "Pflanzen-teratologie," **2**: 59, Genoa, 1894.

posites, especially *Cosmos* and *Coreopsis*. Some of my earliest experiments, undertaken to study the effect of selection on such deviations, yielded negative results. De Vries[23] describes and illustrates a *fistulosa* variety of *Dahlia variabilis* which appeared among his cultures. Among chrysanthemums such "quilled" forms are not rare. "Enterprise" is a variety which illustrates this type and which not infrequently is met with at chrysanthemum exhibitions.

Next to gardens, cultivated fields, *i. e.*, places where a large number of individuals of the same species or variety are grown, offer the best opportunity for the discovery of new or aberrant forms. One only has to be reminded of the case of the beardless Anderbeck oats.[24] In a similar manner there was found, among the numerous alfalfa plants which occupy a large portion of the acreage of the garden, a white-flowered specimen, the flowers of which, on fading, became almost yellow. Since then there were found in a neighboring field, a group of such white-flowered plants.

Color varieties are among the deviations most frequently noted, perhaps because the resulting change is particularly easy of observation. They occur both as to flowers, as for instance in *Lobelia syphilitica alba, Trifolium pratense album,* etc., and as to fruits, as instanced by *Gaylussacia resinosa leucocarpa,*[25] *Vaccinium pennsylvanicum leucocarpum, V. corymbosum atrococcum* f. *leucococcum, V. canadense chiococcum.*[26] White strawberries of course are well known. Yellow-fruited varieties exist of *Ilex myrtifolia*[27] as well as of *Ilex opaca* and *I. verticillata.* The Californian holly, *Heteromeles arbutifolia,* also has a yellow-berried variety.[28] *Calli-*

[23] De Vries, H., "Mutationstheorie," **1**: 480, fig. 134.

[24] De Vries, H., *loc. cit.*, 59.

[25] Porter, Thos. C., "Additions to our Native Flora," *Bull. Torr. Bot. Cl.*, **16**: 21, 1889.

[26] Deane, W., "Albino Fruits of Vacciniums in New England," *Rhodora,* **3**: 263, 1901.

[27] Harper, R., "*Ilex myrtifolia* with Yellow Fruit," *Torreya,* **2**: 43, 1902.

[28] *The American Botanist,* **15**: 49, 1909.

carpa americana and *Rubus cuneifolius* both possess white-fruited varieties.[29]

Of *Solanum nigrum* there exist, besides the black-fruited form, one with yellow and one with green fruit. *Atropa Belladonna* exhibits the same color forms of the fruit which to us are familiar in the cultivated peppers, viz., red and yellow. Finally, in shrubs which are grown chiefly because of the coloring of the bark, for instance *Cornus stolonifera*, with a red bark, there may be met with forms which have a yellow bark. So numerous are references to color varieties in our literature and these variations are met with so often that their frequency suggests facility of origin perhaps parallelled only by that through which dwarf forms are produced. For several years, on collecting trips in the vicinity of St. Louis, Mo., all patches of *Lobelia cardinalis* were examined with particular care for white-flowered plants, since they were known to exist in various parts of the United States. Though these observations did not lead to the desired result, Mr. O. S. Ledman, of St. Louis, was able to find on the peninsula in the northern portion of Pittsburg Lake, St. Clair Co., Ill., opposite St. Louis and in a locality with which I believed myself to be thoroughly familiar and had searched most carefully on several occasions, some plants of *Lobelia cardinalis alba*.

This would indicate that the formation of the white-flowered variety had taken place recently, though the possibility of transportation from other localities, though improbable, is not excluded. That a white-flowered form of *Medicago sativa* is formed as readily seems likely. Various species belonging to the Leguminosæ possess *alba* varieties. De Candolle speaks of a color variety,[30] and at first it was thought the specimens under consideration could be classed here. Since then, however, there were found in the same alfalfa field several

[29] Rolfs, P. H., "Variation from the Normal," *Asa Gray Bull.*, **8**: 75, 1900.

[30] *Medicago sativa versicolor* (Sér. mss.): floribus luteis coeruleisque. *M. falcata versicolor* Wallr. sched. cort., p. 398. *M. lutea-cærulea* hort., *Prod.*, **2**: 173, 1825.

plants which answer the description of the variety mentioned in the *Prodromus,* more or less. It is more than probable that these plants, the flowers of which exhibit a great variation in color, are to be included under the "variegated alfalfas," for which Westgate[31] suggests the designation "*Medicago falcata* × (*M. sativa*), to indicate that "the hybrids have been recrossed several times with ordinary alfalfa and also among themselves." Hybridization, however, does not explain the white color of the flowers. That white-flowered plants and those with flowers of a yellow or cream color are not of rare occurrence is shown by the data furnished by Westgate[32] who notes such plants among four, respectively five of the forms experimented with. On the other hand, in view of the known existence of white-flowered forms the assumption of the formation of the white-flowered plants at Ann Arbor, through recent mutation, does not seem warranted. At the same time, such a possibility is not excluded, for while we do not believe that hybridization can have as its direct result the production of a new character, or the loss of one,[33] it is not at all improbable that hybridization indirectly may cause a plant to initiate a mutation period. It is expected that the seed gathered from the white-flowered plants will, in the course of a generation or two, yield a pure white offspring. This seems to be the experience of others. Mr. C. V. Piper, of the Bureau of Plant Industry, U. S. D. A., in a reply to a recent letter concerning *alba* varieties of *Medicago sativa* says: "Some of

[31] Westgate, J. M., "Variegated Alfalfa," U. S. D. A., B. P. I., Bull. No. 169, February, 1910.

[32] *Loc. cit.*, 37, Table I.

[33] Instances which may suggest themselves but which obviously fall outside our definition, are in the first place those in which atavism comes into play, such as is the case in a cross between *Datura lævis* and *D. ferox.* (Naudin, *Ann. Sc. nat.*, 5 Sér., **3**: 155, 1865. Reciprocal crosses of the two white-flowered plants yielded a uniform offspring with pale purple flowers. (See also de Vries, "Mutationstheorie," **2**: 44, 201.) More recently, through the work of Cuénot, Durham and Nilsson, another, more plausible, explanation of the reappearance of the purple color can be given. (See L. Plate, "Vererbungslehre und Deszendenztheorie," 1910.)

our selections of these white-flowered forms now breed true.''

In connection with this *alba* form I wish to call attention to the local distribution of a white-flowered form of *Solanum Dulcamara,* lately taken into cultivation in the experiment garden. This variety occurs but rarely

FIG. 3. *Arctium minus laciniatum* at Albion, Mich.

in the vicinity of Ann Arbor, chiefly on river and lake shores and in swampy places. But at Albion, Mich., it was found in great abundance, growing in moist situations alongside of the species. While it will take some years to determine the constancy of this variety, there is in my mind no question as to the outcome of the experiment. It is a variety not always recognized in our floras, though evidently met with from time to time.[34] But if we give specific rank to mere color varieties, as we do in the case of *Datura Tatula* and *Datura Stramonium,* why not give taxonomic recognition to the equivalent color variety of *Solanum Dulcamara,* the more so

[34] Collins, F. S., ''A Variety of *Solanum* New to America,'' *Rhodora,* **12**: 40, 1910.

since the addition of such an exceedingly variable character as is pubescence, seems sufficient to bring this about (*Solanum Dulcamara* var. *villosissimum* Desv.)?

The last illustration points to the largest source of new or at least imperfectly known species and varieties, *i. e.*, the native flora. The same rule applies here as in cultivated fields: striking morphological differences most readily attract attention. When the plant normally is possessed of large leaves, as is, for instance, *Arctium minus*, any differences in the foliage become especially noticeable. It is through this fortunate circumstance that we owe to Professor Charles E. Barr, of Albion College, Michigan, the discovery of at least a new locality for the apparently rare laciniate form of the species just mentioned (Fig. 3).

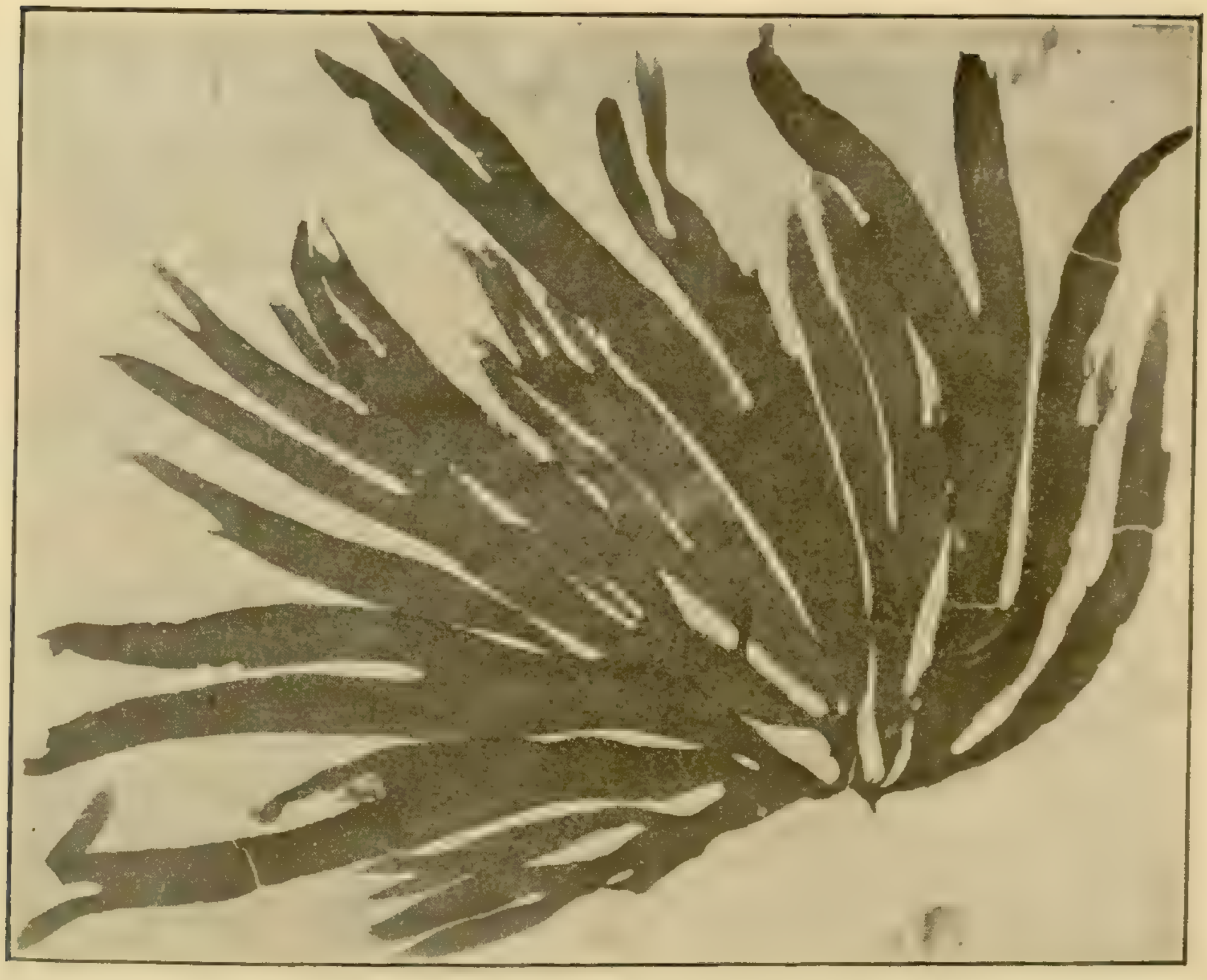
Laciniate forms are of relatively frequent occurrence. We find them not only among the phanerogams and the vascular cryptogams, but even among the algæ one can meet with forms which may be interpreted as such, for instance *Callophyllis furcata* Farlow[35] and *C. furcata* f. *dissecta* Farlow[36] (Fig. 4), though of course there is no connection. One of the earliest accounts of the sudden appearance of a laciniate variety is given by Marchant.[37] In 1715, in his garden, he discovered a plant which, though evidently belonging to the genus *Mercurialis*, was entirely new to him and which did not appear to have been described previously. He named it *Mercurialis foliis capillaceis*. No seed being collected, the next year the same garden spot was anxiously watched. Six plants made their appearance, four of which possessed the character of the plants which had appeared in 1715. The other two were sufficiently different to be segre-

[35] Exsic. in Collins, Holden and Setchell, Phycotheca Bor. Am. Fasc. 18, No. 883, 1901.

[36] Setchell, W. A., and Gardner, N. L., "Algæ of Northwestern America," 306, Univ. Calif. Publ., **1**, 1903.

[37] Marchant, J., "Sur la production de nouvelles espèces de plantes," *Hist. de l'Acad. d. Sc.*, 1719, 57, Paris, 1721.

Marchant, J., "Observations sur la nature des plantes," *Mém. de l'Acad. Roy. d. Sc.*, 1719, 59, pl. 6, 7, Paris, 1721. See also THE AMERICAN NATURALIST, **45**: 493, August, 1911.



a

b

FIG. 4. *Callophyllis furcata* and *C. furcata dissecta.*

gated under the term *Mercurialis foliis in varias et inæquales lacinias quasi dilaceratis*. They were remarkable chiefly because of their laciniate leaves. Both forms appeared to differ from *Mercurialis annua* in having a longer lease of life, since they remained green until the latter part of December. Plants of both continued to appear in 1717 and 1718, propagating themselves.

Masters and others have given lists containing several instances of the appearance of laciniate forms, to whose number one readily may add by glancing over the catalogues annually published by the principal seed houses. It is especially of trees and shrubs (*Acer platanoides laciniatum, Betula pendula* var. *dalecarlia,*[38] *Rubus fruticosus laciniatus*) that cut-leaved varieties are in demand. This popularity is equaled only by that which *Chelidonium majus laciniatum* appears to enjoy in the world scientific, dating from the time when Roze[39] called attention to its history. Laciniation seems to have taken place at least twice in the genus *Chelidonium*. Of *C. japonicum* Thumb. occurs a var. *dissecta*.[40]

There exist several varieties of *Chelidonium majus*. Thus we have the broad-petaled form (*C. majus latipetalum*) of the Groningen Botanic Garden, the double-flowered variety and the cut-leaved one, the latter particularly interesting because the laciniation extends to the petals. During the last four years I have cultivated

[38] A cut-leaved variety of *B. pendula* is also known, *vide* Sanford, S., "A Cut-leaved Cherry Birch," *Rhodora,* **4**: 83, 1902.

[39] Roze, E., "Le *Chelidonium laciniatum* Miller," *Journ. de Bot.*, **9**: 296, 301, 338, 1895.

[40] Prain, D., "A Revision of the Genus *Chelidonium*," *Bull. Herb. Boiss.*, **3**: 570, 1895.

The Papaveraceæ yield other instances of the reappearance of an abnormality in members of the same genus, for instance pistillody of the stamens. The most quoted instance is that of *Papaver somniferum polycephalum*, a variety which was grown more than fifty years ago in the trial grounds of the Vilmorins. Similar varieties were described by von Mohl for *P. orientale* and by Elkan for *P. dubium* (Henri van Heurck, "Notice sur une prolification axillaire floripare du *Papaver setigerum*," *Bull. Soc. Roy. Bot. Belg.*, **2**: 329, 1863) and is said to occur also in *Macleya cordata* (Le Sourd-Dussiples et Georges Bergeron, "Note sur un cas de métamorphose ascendante," *Bull. de la Soc. bot. de France,* **8**: 348, 1861).

eight lots of *Chelidonium majus laciniatum*, two of which have double flowers, the seed being obtained through the exchange lists of various botanic gardens. These eight lots apparently represent five distinct forms. The differences are not great and probably would remain unnoticed by the casual observer. After constant association with them one can not fail to recognize the differences, however slight. But though slight, the differences are constant. They consist in the degree of laciniation as well as in degree of hirsuteness. It might be argued that these differences perhaps are due to differences in external conditions or in the age of the plants or in seasons, etc., just as the leaves produced by *Acer saccharinum* var. *Wieri*, in the latter part of the summer at the extremities of the long, slender twigs, have a lamina far more reduced than those formed earlier in the year. Roze calls attention to the fact that in his cultures of *Chelidonium laciniatum* the degree of laciniation of the leaves increased as the season advanced,[41] the petals undergoing a similar change. He also noted that the degree of laciniation increased with the amount of light received.

While we have noted that the differences between the varieties are most marked in the early part of the year, the fact that our cultures were carried out under uniform conditions as to soil, light and water supply, and that the various types are recognizable even in the late summer, seems to indicate that these forms are entitled to varietal rank. The specimen illustrated in Fig. 5 ought to set at rest all doubts upon this point. One hardly would care to account for the extreme reduction of leaf surface in this case on the basis of the influence of fluctuating variability. This form, in all probability, is identical with the *Chelidonium majus foliis et flore minutissime laciniatis* of the Hortus regius (1661), which

[41] Roze, *loc. cit.*, 339. "... si l'on suit la plante dans sa croissance, on remarque que les deux ou trois premières feuilles (après les feuilles germinatives) ont l'apparence de celles de la forme *crenatum* et les dernières celles de la forme *fumarifolium*, mais a découpures plus courtes et moins étroites."

originated in the Paris Botanical Garden from seed of *Chelidonium majus laciniatum* and to which de Candolle afterwards gave the name *C. laciniatum fumariæfolium*.[42]

A second plant in our garden represents an extreme in another direction and is intermediate between the

FIG. 5*a*. *Chelidonium majus*.

species and the variety *laciniatum*. It probably is identical with the var. *crenatum*.[43] Besides these three varieties I believe to be able to distinguish two other forms, constant from seed. It is possible that all of them originated through mutation of *C. majus laciniatum*, as did the variety *fumariæfolium*. It is equally possible that laciniate forms of *Chelidonium majus* have originated

[42] *Prod.*, 1: 123.

[43] *C. majus crenatum* Lange, Fl. dan.

more than once and directly from the parent species. This is the view taken by Clos,[44] who describes the finding by P. Barthès of a plant of *C. majus fumariæfolium* in Sorèze, Tarn. It is to be noted that these plants bore underdeveloped, seedless pods. This last seems to speak

FIG. 5b. *C. fumariæfolium.*

in favor of the assumption of a *creatio de novo*, since plants from other stock appear fertile. To this extremely interesting point, a discussion of which falls outside the scope of the present paper, I hope to return in an article shortly to be published.

The correctness of the view that the same mutation or at least a mutation in the same general direction may take place in different stocks, must be granted *a priori*. Evidence in the support of this belief we find in the ex-

[44] Clos, D., "Réapparition de la Chélidoine a feuille de Fumeterre," *Compt. rend.*, **115**: 381, Paris, 1892.

istence of several distinct laciniate forms of different species of trees and shrubs. The varieties *heterophylla, laciniata, asplenifolia*[45] and *incisa* of *Fagus sylvatica, Alnus glutinosa laciniata, A. glutinosa quercifolia* and *A. glutinosa oxyacanthifolia* are instances to which numerous others might be added. It would seem that the laciniate forms of *Mercurialis annua,* observed by Marchant, would find a place here.[46]

The repeated sudden appearance of the same variety has been noted by various authors. Darwin, Korschinsky,[47] the late director of the St. Petersburg Botanic Garden, and de Vries[48] give numerous instances. Thiselton Dyer was able to show the repeated formation of at least two new varieties of *Cyclamen latifolium.*[49] Many, from personal experience, will be able to supply other instances. And while most of the cases which come to our notice probably are explainable through accidental transportation of seed or through Mendelian splitting of a hybrid between the species and a retrograde variety or through atavism,[50] there are others which do not admit

[45] This variety, like cut-leaved varieties of other species, not infrequently shows atavism in certain shoots. See de Vries, "Atavismus durch Samen und durch Knospen" ("Mutationstheorie," **1**: 482), and also R. G. Leavitt, "Partial Reversion in Leaves of the Fern-leaved Beech," *Rhodora,* **6**: 45, 1904; O. Paulsen, "Blivende Axelblade hos Boegen," *Bot. Tidskr.,* **24**: 281, 1902; A. Trotter, "Contributo alla teratologia vegetale," *R. S. Bot.,* Italy, **44**, 1902.

[46] This variation in the degree of laciniation within a single species ought to throw some light on "unit-characters." If we consider—as I believe generally is done—laciniation to be a "unit-character" it would seem that such a "unit-character" may be subject to considerable variation, though the degree of variation is constant or at least approximately so for each individual case. This relative stability of the varietal character of course does not prevent the extremes of each degree of variation from overlapping.

[47] Korschinsky, S., "Heterogenesis und Evolution," *Flora,* **89**, 240, 1901.

[48] "Species and Varieties," 627.

[49] Thiselton Dyer, W. T., "The Cultural Evolution of *Cyclamen latifolium,*" *Proc. Roy. Soc.,* **61**: 135, 1897. See also J. Denman, "The Sporting Peculiarity of the Persian Cyclamen," *Gard. Chron.,* 3d Ser., **29**: 266, 1900.

[50] Among the plants cultivated in the experimental grounds of D. M. Ferry & Co., of Detroit, Mich., is a variety of cabbage bearing the name

of such an interpretation. Thus the finding by Mr. W. H. Ransome, of several plants of the four-leaved variety of *Fragaria vesca* at a point about twenty miles west of Kalispel, Flathead Co., Mont. A new form, which has appeared at various times and which because of the nature of the variation is incapacitated from reproducing itself by seed, would from this very fact constitute an ideal illustration of repeated mutation, since a hybrid origin of the individuals which appeared later, is excluded. Such an instance is yielded by the wheat-ear carnation, *Dianthus Caryophyllus imbricatus*. A sterile variety, it is propagated vegetatively. First described in the eighteenth century, and since then the subject of comment on the part of several teratologists, its sudden appearance has been noted in different stocks and at various times and places.[51] Instances of similar malformations may be met with from time to time. Thus Ballard[52] describes a sunflower in which the flowers were replaced by scales.

It is a question whether the plants of *Arctium minus laciniatum* from Albion are to be considered as derived from preexisting plants of the variety or whether they have arisen *de novo*. Are they perhaps the result of a mutation of *Arctium minus?* Plants of both the species and the variety were found growing near the junction of Hannah St., Albion and the Kalamazoo River. The road at this point is bordered by a tall fence between which and the sidewalk is a space about 1½ feet in width. In a strip about 45 feet in length, among other weeds and with several specimens of the species, were found about a dozen individuals of *Arctium minus laciniatum*. Five of these were two-year-old plants, the remainder young rosets. As far as could be judged at the time, but slight differences exist between the leaves of the rosettes of the species and of those of the variety. A slight tendency

"Early Winnigstadt." For the last eight or ten years from one to three per cent. of "Green Glazed" have appeared among them.

[51] De Vries, H., "Species and Varieties," 228, 1905.

[52] *Gard. Chron.*, 3d Ser., **30**: 347, 1901.

to laciniation is all that could be observed. Perhaps the result of the cultural experiments, when a large number of rosettes can come under observation, will shed more light upon this point. But there was no danger of confusing the adult plants of the species and of the laciniate variety, for the latter presented a most striking appearance (Fig. 3). At first glance it seemed as if caterpillars or grasshoppers had destroyed the greater part of each leaf; the midrib and larger veins and here and there a small portion of the blade being left. A closer examination revealed the fact that the rosette leaves differed least from those of the normal plant. The leaves *a* and *b* in Fig. 6 show this sufficiently. The latter represents a

FIG. 6. *Arctium minus* and *A. minus laciniatum*. *a*, rose leaf of the species; *b–k*, leaves of the variety; *l*, *m*, inflorescences of the variety.

rosette leaf of the var. *laciniata*, the former one of the species. The next leaves possess a marked laciniation (Fig. 6 *c*, *d*, etc.). As one proceeds higher up the stem, the laciniation becomes more pronounced, till finally but a figment is left of the leaves in the region of the inflores-

cence. In fact, there are leaves which possess a midrib only.

What appears to have been the same plant has been described in a recent publication,[53] as occurring in two different places about Joliet, Ill., and near Champaign, Ill. Here the inflorescence is referred to as "irregular with numerous small sterile flowers." It is also reported from South Bend, Ind.[54] Previously its appearance had been noted near Jessup, Ind.[55] Here also the inflorescence is described as "irregular, heads numerous, mostly small, rudimentary and apparently sterile." From an article by Fernald and Wiegand[56] it is gathered that Darlington in his "Flora Cestrica" referred to a similar plant.[57]

To Professor Fernald, who saw Darlington's specimen in the Gray Herbarium, I am indebted for the following: "Darlington's sheet bears the note: var. foliis pinnatifidis vel potius grosse dentatus. West Chester, Pa., August 25, 1858. These are imperfect specimens of the plant referred to in Fl. Cestrica, p. 156; but I am not sure that it is the one spoken of in Gray's Manual. The inflorescence always has a kind of half-starved or semi-abortive appearance. W. D."

The general appearance of the inflorescence certainly suggests a teratological development, giving an impression similar to that caused by inflorescences of *Rhus glabra* infested with a certain gall. But an examination of the living plants, at least such was the case with those at Albion, at once does away with any question as to their normal condition. The peculiar ragged appearance of the flowering shoots is merely due to a progres-

[53] *The American Botanist,* **15**: 83, 1909.

[54] *The American Botanist,* **15**: 112, 1909.

[55] Brown, H. B., "A Peculiar Specimen of *Arctium*," *Plant World,* **12**: 135, fig. 2, 1909.

[56] Fernald, M. L., and Wiegand, K. M., "A Synopsis of the Species of *Arctium* in North America," *Rhodora,* **12**: 43, 1910.

[57] Darlington, W., "Flora Cestrica," 436, 1837. "A variety has been observed here, occasionally, with pinnatifid leaves." Perhaps the references to a variety with pinnatifid leaves met with in Wood's Flora and in the earlier editions of Gray's "Manual" owe their origin to this note.

sive laciniation as the leaves approach the apex, comparable to the seasonal reduction of the blades in *Acer saccharinum* var. *Wieri,* or of the various laciniate varieties of *Chelidonium majus* referred to above. Also, Professor Barr was able to gather seed. It should be stated in this connection that while the seed of the species, obtained from Albion, germinated readily and produced typical *Arctium* seedlings, there appeared in the seedpans devoted to the variety, seedlings having all the characteristics of those of *Lactuca Scariola integrata,* and these only. Seedlings of species and their varieties are as a rule so much alike that the thought at once presented itself that some seed of the wild lettuce either had become mixed with the seed of the variety or was contained in the soil used for growing the seedlings. Were either of these suppositions correct, it would seem curious that the same thing had not occurred in the case of the seed of the species. At least one of these possibilities could have been eliminated had it been possible to sow the seed in sterilized soil. As the rosettes grow older there could be no doubt as to their really belonging to *Lactuca.* While therefore these experiments yielded negative results, it still is possible that their repetition, with perhaps certain modifications, may result differently. Also an attempt should be made to obtain seed from a different source, for it is very well possible that while one lot of laciniate-leaved plants is fertile, another, perhaps of distinct origin, is sterile. We find an analogy in the case of *Chelidonium majus laciniatum* quoted above.

Unfortunately but few herbarium specimens are available for comparison with the specimen of Darlington in the Gray Herbarium. Through the courtesy of the curators of the herbaria mentioned we learn that in the herbarium of the Smithsonian Institution the variety is represented by a single specimen "collected by Alfred E. Ricksecker at Elyria, Lorain County, Ohio, August 1, 1894." It is added that it has very deeply laciniate leaves and that the venation is very different from that

of the common form. In both these respects it agrees with the Albion specimens.

From the herbarium of the New York Botanical Garden, Dr. Marshall A. Howe was kind enough to write: "We have in our herbarium apparently only one specimen of the form that you have in mind." This specimen was collected in 1865 at Uxbridge, Mass., by J. W. Robbins. Another sheet of this material is in the Gray Herbarium.

Through the courtesy of Professor William Trelease we know that a laciniate-leaved variety of the burdock is represented in the herbarium of the Missouri Botanical Garden by two herbarium sheets, the one, without date, bearing a specimen collected in Europe, the other a specimen collected at New Bedford, Mass., in 1890 by Harvey. Professor Trelease adds: "Neither has represented the extreme cutting of the leaves that yours shows, but there is enough of it to lead me to think that as extreme forms might have been collected."

Dr. Greenman, of the Field Museum of Natural History, fails to identify any material in this collection with *A. minus laciniatum*, "unless possibly a very poor specimen collected at Chelsea, Mass., Sept. 24, 1863, by J. Blake."

While it is probable that the same form occurs in Europe, thus far it does not appear to have been recorded in the floras. Inquiries on the part of my friend Dr. Jongmans, of the State Herbarium at Leyden, Holland, failed to elicit confirmatory answers, nor does the variety appear to be represented either in the Leyden herbarium nor in any of the European herbaria whose curators I have been able to consult.

It is hoped to amplify, by further inquiries, these somewhat meager data. From what we know at the present time, it would appear that *Arctium minus laciniatum* is of comparatively rare occurrence (Fig. 7). I have never met it except at Albion, though a good deal of territory was covered both here and abroad and I was looking for just such variations. Professor Barr, who has

botanized extensively in the vicinity of Albion, never has encountered it. From a glance at the map it appears not improbable that this plant, perhaps having its origin in Massachusetts, or introduced there from Europe,

Distribution of *Arctium minus laciniatum.*

Fig. 7. Map, showing successive collection of *Arctium minus laciniatum* in the United States, 1837-1910, and based upon the data available at the present time.

1.	Chester Co., Pa. 1837	6.	Jessup, Ind. 1907
	West Chester, Pa. 1858	7.	South Bend, Ind. ..... 1909?
2.	Chelsey, Mass. 1863	8.	Joliet, Ill. 1909
3.	Uxbridge, Mass. 1865	9.	Champaign, Ill. 1909
4.	New Bedford, Mass. 1890	10.	Albion, Mich. 1910
5.	Elyria, Ohio 1894		

perhaps in ballast, gradually has been transported to various points of the compass, the area being covered by it being limited to the northeastern section of the United States. The transportation of seed, provided this is formed at all, is not unlikely. Fairly large gaps, though, appear between certain of the dates of collection. Thus, the plant does not appear to have been collected between 1837 and 1858, between 1865 and 1890, between 1894 and 1907, gaps, respectively, of eleven, fifteen and thirteen years. Yet these lacunæ very well may be accounted for on the one hand by the failure of botanists to collect the

"abnormal" specimen and on the other hand by the lack of data at our command.

There will not be wanting those who are inclined to look upon the Albion specimens as well as upon those from other localities as having originated through mutation. The mutation idea, however, involves the idea of constancy. Will the laciniate form come true to seed? If the laciniate plants at Albion are mutants one ought to be able to get a certain percentage of laciniate plants from the apparently normal plants in the same locality, eliminating in the experiment all possibility of hybrid origin. Experiments to determine this have been inaugurated, but at least four or five years must elapse before their results can be communicated. In view of our experience with other laciniate forms and provided the variety produces good seed, the question can hardly be answered in the negative, though in view of the opinions expressed by others we must reserve our decision until the question has been answered by the plant itself. For this is, after all, the only method which, though perhaps tedious at times, will lead to a sane and safe conclusion. Those in sympathy with this idea realize one need not go far from home to find material as abundant, as interesting, as instructive, as important, as can be met with at a greater distance. And while the exploration of new or difficultly accessible regions offers many attractions, he to whom such an opportunity is not given need not feel slighted, for work nearer home offers the advantage of greater facility, especially of observation. Working along lines similar to those followed by de Vries, Veit Wittrock, Dahlstedt and Nillson, it is to the botanic garden we must look for a solution of our problems.

SOME EXPERIMENTAL OBSERVATIONS CONCERNING THE BEHAVIOR OF VARIOUS BEES IN THEIR VISITS TO COTTON BLOSSOMS. II

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Experiment No. 21.—July 29. Observations continued one half hour, from 1:30 to 2:00 P.M. Three blossoms arranged in the same row.

(*a*) Control. Normal American upland cotton blossom pinned in position.

(*b*) Control. Normal American upland cotton blossom pinned in position.

(*c*) *Hawasaki* blossom entire pinned in position.

DATA FOR EXPERIMENT NO. 21

Position of Blossom	Total Inspections	Distribution by Species						Total Entrances	Distribution by Species					
		Melissodes sp.	*Elis plumipes*	Honey Bees	Butterfly	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Elis plumipes*	Honey Bees	Rutterfly	Bumble Bees	Unidentified Bees
(*a*)	12	10		2				1			1			
(*b*)	9	6		3				2			2			
(*c*)	11	8		2	1			2	1			1		

Experiments 18, 19, 20 and 21 are essentially similar, since in each a blossom of the Asiatic cotton, *Hawasaki,* is compared with American upland blossoms. The points of location of the blossoms were unchanged throughout, but the blossoms themselves were interchanged in order to check any advantage which might obtain from a particular position in the arrangement.

The *Hawasaki* blossom is smaller in size than the upland and much brighter yellow in color with conspicuous deep reddish purple petal spots inside. It was thought

that the behavior of visiting bees toward the American upland blossoms and the dissimilar Asiatic *Hawasaki* would perhaps serve to distinguish between the effects of color and form as compared with odor in inducing the visits of bees into cotton blossoms. Results indicate that the *Hawasaki* blossom, although quite unfamiliar to our native bees, is nearly as frequently inspected as our American upland blossoms.

From the readiness with which bees are led to inspect the *Hawasaki* blossoms, single detached cotton petals and the white convolvulus blossom even after it had become greatly wilted and collapsed, it is evident that they are not at first sight led to distinguish cotton blossoms from other blossoms, etc., by their characteristic form and color alone. Only by a nearer approach does the process of inspection become more discriminating in its nature with regard to the kind of blossom.

Experiment No. 22.—July 29. Period of observation one half hour, from 2:10 to 2:40 P.M. Two blossoms were used on two adjacent plants in the same row and similarly exposed.

(*a*) Blossom of American upland which had opened the day before and in consequence had become deep reddish purple in color.

(*b*) Control. Normal, recently opened cream-colored blossom of same variety.

DATA FOR EXPERIMENT NO. 22

Position of Blossoms	Total Inspections	Distribution by Species					Total Entrances	Distribution by Species				
		Melissodes sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	12	11				1						
(*b*)	26	24			2		1	1				

Some time after midday, depending upon prevailing weather conditions, the recently expanded cream-colored cotton blossoms of that day slowly begin to close again and assume a reddish color, which by the second day is a

deep reddish purple. In connection with previous observations it was noted that those older blossoms appeared to possess little attractiveness for bees. The test was designed to reveal any differences which might serve to indicate to the bees that the purple blossom had passed the stage of usefulness to them. Although bees may in their flight indicate that the red blossom has been perceived, the inspections are usually far briefer than with the newly open blossoms of the same day. Rarely does a bee noticeably check its flight to hover over the red blossoms in the careful manner that it usually inspects those newly opened blossoms which are unchanged in color. The marked difference in color or some peculiarity of odor seems to inform the bees that an old blossom has nothing to offer them, since the pollen has been scattered and nectar is no longer secreted.

Experiment No. 23.—July 30. Time of observation one half hour, from 9:00 to 9:30 A.M. Three blossoms are arranged in the same row in equally exposed positions, as in previous experiments.

(*a*) Control. Normal upland cotton blossom pinned in position.

(*b*) Control. Normal upland cotton blossom pinned in position.

(*c*) Normal upland cotton blossoms with a drop or two of honey at base of petals within.

DATA FOR EXPERIMENT NO. 23

Position of Blossoms	Total Inspections	Distribution by Species					Total Entrances	Distribution by Species				
		Melissodes sp.	*Elis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Elis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	7	5			1	1	1				1	
(*b*)	6	2		1	2	1	1				1	
(*c*)	7	4		1	1	1	2	1		1		

The presence of a small quantity of honey in the blossom at (*c*) has not noticeably increased the number of entrances into it.

The single *Melissodes* which entered the blossom at (*c*) gave evidence of its appreciation of the honey which it discovered by stubbornly refusing to leave the blossom until rather violently brushed away.

Experiment No. 24.—July 30. Time of observations one half hour, from 11:00 to 11:30 A.M. Three blossoms arranged in same row. This experiment is an exact repetition of the preceding.

(*a*) Control. Normal upland cotton blossom pinned in position.

(*b*) Control. Normal upland cotton blossom pinned in position.

(*c*) Normal blossom with honey at base within.

DATA FOR EXPERIMENT NO. 24

Position of Blossoms	Total Inspections	Distribution by Species					Total Entrances	Distribution by Species				
		Melissodes sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	26	16	2	4	3	1	7	3	2		2	
(*b*)	33	22	2	5	3	1	8		2	3	3	
(*c*)	14	9	1	3	1		0					

Experiment No. 25.—July 30. Time of observations one half hour, from 11:30 to 12:00 A.M. Three blossoms arranged in the same row.

(*a*) Normal cotton blossoms pinned in position as a control.

(*b*) Normal cotton blossom with honey added at base of petals within.

DATA FOR EXPERIMENT NO. 25

Position of Blossoms	Total Inspections	Distribution by Species					Total Entrances	Distribution by Species				
		Meltssodes sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	22	16		6			4			4		
(*b*)	19	14		4	1		1			1		
(*c*)	15	10		3	2		2			1	1	

(*c*) Normal cotton blossom pinned in position as a control.

During the forenoon the weather was dull, so that bees were less frequent in their visits.

Experiment No. 26.—August 1. Period of observations one half hour, from 9:00 to 9:30 A.M. Blossoms arranged in same row as follows:

(*a*) Normal cotton blossom with honey at base of petals within.

(*b*) Normal cotton blossom pinned in position as a control.

(*c*) Normal cotton blossom pinned in position as a control.

DATA FOR EXPERIMENT NO. 26

Position of Blossoms	Total Inspections	Distribution of Species					Total Entrances	Distribution of Species				
		Melissodes sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	26	22	1	1	1	1	0					
(*b*)	27	22		2	1	2	1			1		
(*c*)	20	17			1	2	1				1	

Experiment No. 27.—August 1. Period of observations one half hour, from 9:00 to 9:30 A.M. Blossoms are arranged in the same row.

At (*a*) an unmutilated cotton blossom was pinned in position. Portions of cotton leaves were carefully cut out and fastened outside and within the blossom in such a manner as to extend just to the margin of the petals on both sides. In this way none of the yellow color of the petals remained visible. The stamen tube, pistil, etc., projected as in a normal blossom. The blossom was practically without petals, since these were not visible, although such odors as they may have possessed could still diffuse around the blossom. A drop or two of honey was also added at the base of the petals within in order to make certain that agreeable odors were present, since

these must now necessarily constitute the sole allurement.

At (*b*) normal blossom pinned in position. The tips of the petals were lightly smeared with honey.

At (*c*) control. Normal cotton blossom pinned in position.

DATA FOR EXPERIMENT NO. 27

Position of Blossoms	Total Inspections	Distribution by Species					Total Entrances	Distribution by Species				
		Melissodes sp.	*Elis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Elis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	0											
(*b*)	34	23		10	1		2			2		
(*c*)	25	14		10	1		6			6		

As shown in previous experiments, the removal of the petals no longer advertises a cotton blossom to the notice of bees. The same results are obtained when the petals are no longer visible, although still attached to the blossom as at (*a*). It is natural to suppose that the presence of honey would add appreciably to the zone of alluring odors surrounding the blossom.

Without the conspicuous corolla to invite inspection, however, the bees are not led to approach sufficiently near to discover the blossom by its attendant odors alone. These results are not in agreement with some of the general conclusions of Plateau in his noteworthy memoirs: "Comment les fleures attirent les insectes." He states: "Les insectes visitent activement les inflorescences qui n'ont subi aucune mutilation mais dont la forme et les couleurs sont masquées par des feuilles vertes."[3] This would follow only when other attractive influences were actively operative, as various odors agreeable to bee visitors.

Experiment No. 28.—August 1. Time of observation one half hour, from 9:30 to 10:00 A.M. This experiment makes use of most of the material and the same positions of the preceding, with the changes as follows:

[3] *Bulletin de l'Académie royale des Sciences*, No. 11, November, 1895.

(*a*) Outer leaf covering removed from the blossom used at (*a*) in preceding experiment, thus making the outer surface of the petals visible. Honey at the base within, as before.

(*b*) Normal blossom pinned in position as a control. No honey has been added to this blossom.

(*c*) Normal blossom used in preceding experiment with petals removed.

DATA FOR EXPERIMENT NO. 28

Position of Blossoms	Total Inspections	Distribution by Species					Total Entrances	Distribution by Species				
		Melissodes sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	9	3		6			0					
(*b*)	11	4		5	1	1	1			1		
(*c*)	1			1			0					

By the removal of the outer covering of the blossoms at (*a*), which in the previous experiment received no inspections, it became nearly or quite as attractive as the control at (*b*). The blossom at (*c*), however, no longer afforded means of attracting the bees. In this experiment and the previous one the corolla at (*a*) was concealed with portions of cotton leaves to guard against introducing repellent odors which may have attended the use of any other material. In the course of this experiment the number of bees flying about became much reduced toward ten o'clock, although the day was clear, hot and sunny. The writer was even forced to postpone his observations for the remainder of the forenoon owing to the scarcity of visiting bees.

Experiment No. 29.—August 1. Period of observation one half hour, from 2:00 to 2:30 P.M. The material is arranged in the same row.

At (*a*) a cotton bud not due to open until the next morning had its petals quite fully pulled open so as to resemble a naturally opening blossom.

At (*b*) a second cotton bud due to open the next morning had its petals partly pulled open.

At (*c*) a normal cotton blossom growing *in situ* as a control.

DATA FOR EXPERIMENT No. 29

Position of Blossoms	Total Inspections	Distribution by Species					Total Entrances	Distribution by Species				
		Melissodes sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Ellis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	15	5		10			0					
(*b*)	2			2			0					
(*c*)	24	4		20			14			14		

In this experiment it was intended to observe the behavior of bees toward immature buds at (*a*) and (*b*) in comparison with fully expanded, mature blossoms. It was assumed that the former, owing to their immaturity, would perhaps prove less attractive to bees through the sense of smell than the fully matured blossoms. Although not definitely proved, it is reasonable to suppose that the processes of active nectar secretion simultaneously attend the unfolding of the petals and the shedding of the pollen. It would then follow that the odor of the unopened buds at (*a*) and (*b*) would prove less alluring than the blossom at (*c*).

The yellow petals of the blossom at (*a*) have served to invite frequent inspection, although at (*b*) this is not as evident. This difference may depend upon the fact that the bud at (*b*) was much less conspicuous, since the petals have been only slightly pulled open. Whatever the true explanation, the mature, fully unfolded blossom which serves as a control at (*c*) has received many more inspections, nearly 60 per cent. of which are actual entrances.

Experiment No. 30.—August 2. Period of observation one hour, from 9:30 to 10:30 A.M. Two blossoms were arranged in the same row in equally conspicuous positions.

At (*a*) a very clean, thin 5×7 glass plate was sup-

ported in front of a fully opened cotton blossom pinned in position. The surrounding cotton leaves were then carefully drawn in closely around the plate so as to overlap the edges and most of the glass surface. In this arrangement, although the blossom was plainly visible through the glass, only a small portion of the glass surface remained in view.

At (*b*) control. A fully opened cotton blossom was pinned in position.

DATA FOR EXPERIMENT NO. 30

Position of Blossoms	Total Inspections	Distribution by Species					Total Entrances	Distribution by Species				
		Melissodes sp.	*Elis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees		*Melissodes* sp.	*Elis plumipes*	Honey Bees	Bumble Bees	Unidentified Bees
(*a*)	18	6		3	4	5	0					
(*b*)	37	20	1	7	4	5	9			5	4	

Of those bees which attempted to inspect the blossom at (*a*), eight flew more or less forcibly against the glass, including two small unidentified bees, one *Bombus* sp., two honey bees and three *Melissodes*. One small bee tried persistently several times to fly through the glass toward the blossom just behind it. It is at once obvious that the blossom at (*a*) invited inspection by passing bees solely through the sense of sight.

Experiment No. 31.—August 9. Observations continued one hour, from 9:00 to 10:00 A.M.

Two blossoms were used in the same row as before. A box of thin wood was carefully constructed for this experiment. The dimensions were such that both cover and bottom were made of thin clear glass by using for each a 5×7 glass plate. These plates fitted tightly in lateral grooves. The box was about 4 inches deep, so that the end of a cotton branch together with its leaves and blossoms could be carefully pushed into a natural position within. By sliding the glass cover into place the box became practically air-tight. The blossom was plainly visible to passing bees, although any attractive

odors which it diffused could no longer act as allurements. When placed in position among the cotton limbs the box and glass were almost completely concealed by drawing in and fastening around it a number of the surrounding leaves. This box enclosed the blossom at (*a*).

At (*b*) control. A natural blossom pinned in position. The blossom at (*a*) received only two inspections, both by small, unidentified bees. The blossom at (*b*) received only five inspections, three being by *Melissodes* and two by honey bees. There were no entrances at (*b*).

Experiment No. 32.—August 9. Observations continued for one half hour, from 10 to 10:30 A.M. This experiment was identical with the preceding, except a third artificial blossom was added.

(*a*) Same blossom enclosed in the glass case as used at (*a*) in Experiment 31.

(*b*) The same control blossom pinned in position.

(*c*) An artificial paper blossom of crepe paper simulating a cotton blossom in color.

The blossom at (*a*) received one inspection by a *Melissodes* which hovered in front of the glass a few seconds only.

(*b*) Received eight inspections, which include two entrances by honey bees. The six inspections were entirely by Melissodes. Three bees inspected the artificial paper blossoms at (*c*), including one each by a *Melissodes*, an unidentified bee, and a honey bee, which paused for a few seconds over the blossom but did not enter. During the last few days bee visitors have been rather too infrequent for satisfactory work, probably in part owing to the partly cloudy forenoons.

Experiment No. 33.—August 11. Observations continued for about one half hour, from 9:00 to 9:30 A.M. Three blossoms are arranged in a row.

At (*a*) three petals were placed in position on a leaf which was spread out flat and held between two thin clean 5×7 glass plates bound firmly together. This was placed in position among the branches of a plant and was nearly concealed by overlapping around it a number of cotton

leaves. In this arrangement the yellow petal color still remained perceptible to the visual powers of bees.

At (*b*) the detached petals of a cotton blossom were enclosed in a 250-c.c. graduated flask which was stoppered and fastened among the cotton leaves. The yellow petals were plainly visible through the clear thin glass of the flask.

At (*c*) a normal cotton blossom as a control.

(*a*) Received no inspections.

(*b*) Received one inspection by a honey bee which touched the flask.

(*c*) Received three inspections by honey bees. Two bees did not enter the blossom but alighted outside to get at the extra-involucral nectaries. During this experiment the bees were too infrequent visitors to make any results conclusive.

Experiment No. 34.—August 12. Time of observations 45 minutes, from 1:30 to 2:15 P.M. This experiment was an exact duplicate of the previous one.

(*a*) Petals of cotton blossom on a leaf between glass plates as at (*a*) in Experiment 33.

(*b*) Petals of cotton blossoms enclosed in a flask as at (*b*) in Experiment 33.

(*c*) Normal blossoms growing *in situ* as a control.

The blossom at (*a*) was twice inspected by *Melissodes*. The petals in the flask at (*b*) were inspected two times by bees, once by a honey bee and once by a small, unidentified bee. The blossom at (*c*) was inspected six times, including five entrances. One inspection was made by a small, unidentified bee, four entrances were by honey bees, and one entrance by a *Melissodes*.

For several days it was rather difficult to secure satisfactory data, as the bees were much less frequent visitors. The species of *Melissodes*, which were extremely common at the beginning of the experiments finally became far less common, although honey bees greatly increased. It is very interesting to note that many honey bees finally began to confine their visits solely to the outer involucral nectaries instead of entering the blos-

soms. This change of habit seemed to become quite general at about the same period, for the writer noted it in all parts of the cotton field.

Throughout the period of observations the bees by their behavior and varying numbers showed themselves extremely sensitive to atmospheric changes, temperature relations, air movements, moisture, sunshine, etc. At times conditions even too obscure for human perception may have regulated their activities. The composition of the bee fauna to be observed in cotton fields shows much variation, depending upon the time of day, prevailing weather and seasonal influences. The position and exposure of the cotton field with relation to various local physiographic features, as type of soil, nearness to woods, swamps, hills and other crops also greatly influence the relative numbers and kinds of bees.

While carrying on his observations the writer noted that the bees, *Melissodes,* were exceedingly abundant among cotton grown on certain heavy, red-clay soils. These bees were much less abundant in fields on the lighter, sandy loams in some other localities. Honey bees are especially noticeable near bee trees or domestic hives. The marked abundance of other bees in particular localities likewise probably depends upon the proximity of the plants to their favorite breeding places.

Nectar glands are especially abundant on the cotton plant, including the leaves as well as the blossoms. The blossoms are supplied with several sets of nectaries. Cotton blossoms with their abundant supplies of readily accessible pollen and nectar and their open structure exclude few insect visitors. It follows that a considerable number of species of bees, wasps and other insects are at all times especially common visitors among cotton blossoms.

During the time the experiments previously described were in progress nearly 2,000 bees were observed to perceive, inspect or enter the blossoms and other material involved. 1,645 of these visits were distributed as follows: 1,381 or 83.9 per cent. were by species of *Melis-*

sodes. 130 or 7.8 per cent. were by honey bees. 40 or 2.4 per cent. were by bumble bees. 83 or 5 per cent. were by various unidentified bees.

Eleven visits were made by *Elis plumipes* and one by a large butterfly. The size and yellow color of the petals serve to make cotton blossoms particularly conspicuous in contrast with their shaded background of dark green foliage. Once visiting insects have entered a cotton field, there is little doubt but that their visual powers almost wholly enable them to discover the blossoms. This is indicated by those experiments where the corolla of certain blossoms has been covered or entirely removed, since following this procedure the remaining portions of the blossoms were unvisited. The size and general appearance of cotton blossoms do not appear to be of great importance in initiating the process of inspection, since a single petal may receive as many inspections as the control. It is of interest to note in this connection that in experiments 14 and 15 the bees did not discriminate between the white convolvulus and cotton blossoms at least until after closer inspection. When such artificial material as cloth or paper was used, although the color more or less resembled cotton petals, the bees were rarely induced to inspect it closely. This discrimination may depend upon perceptible differences in color and texture rather than the presence of repellent odors which the material possessed. Many eminent observers have adduced a great deal of evidence which proves beyond doubt that bees develop keen powers of discernment in their associations with the structural details of different flowers.

The actual number of entrances into cotton blossoms is small in comparison with those instances when blossoms have been merely perceived or inspected. The writer's observations show that of 1,061 inspections of the control blossoms only 129, or 12.1 per cent., were actual entrances. One hundred and twenty of these entrances were distributed among the several kinds of bees, as follows: 45, or 37.5 per cent., were by *Melissodes;*

45, or 37.5 per cent., were by honey bees; 6, or 5.0 per cent., were by *Elis plumipes;* 16, or 13.3 per cent., were by bumble bees; 8, or 6.6 per cent., were by various small unidentified bees. A single entrance was made by a large butterfly.

Although it seems clear that the corolla of cotton blossoms invites the first approach of the bees through their visual sense, it is not so easy to determine the relative importance of the sense of sight and smell involved in their nearer inspections. Just why do so few bees decide to enter? In their careful inspection of a single petal or a suspicious blossom is the sense of sight alone involved? Except for a single *Elis plumipes*, no bee has ever alighted upon detached cotton petals, although these have served to attract attention quite as often as the control blossoms. It is not unusual, however, for the bees to inspect these structures very intently, almost touching the surface in their movements over them. The bees have just as persistently refused to enter all artificial blossoms or blossoms mutilated by removing a part or all of the petals. In experiment 6 a bee was completely deceived by the unreal structure at (*c*) made to simulate an expanding bud by the use of actual cotton petals and portions of a cotton leaf. In this instance the bee inspected and finally squeezed itself down between the petals. Unless the fresh petals themselves possess a characteristic odor, odors such as might emanate from a normal blossom were entirely lacking and, therefore, could not have induced the bee to enter. Plateau concludes that visual conspicuousness by means of bright colors is of no advantage whatever to blossoms so far as insect visitors are concerned. He claims that if in nature all blossoms were green like the surrounding foliage, they would be just as readily discovered by bees and other insects in virtue of their odor. The writer's experiments in the field indicate that conspicuousness in virtue of their position and yellow coloration is a very important factor in leading bees and other insects to perceive cotton blossoms.

It does not appear that the addition of small quantities of honey either upon the petals themselves or at the base of the flower within appreciably increased the inspections or entrances, although if a bee chanced to discover this honey, its fondness for it was evinced by its strong reluctance to leave.

It is probable that the inspections are largely of a visual nature, though these may be supplemented by certain odors when the blossoms are more closely examined. Many noted observers, especially Müller, have adduced abundant evidence to prove that the visual power of bees becomes very critical in their behavior toward minute differences of floral structure.

The bee *Melissodes bimaculata,* which is probably by far the commonest of this genus in certain cotton fields at Thompson's Mills, behaves somewhat differently from other bees in its inspections. Its flight is swift and irregular, and its entrance into a blossom is usually preceded by a more careful examination than that resorted to by bumble bees, the common honey bee, or the wasp *Elis plumipes.* It is the usual procedure for the last to fly straight into a blossom or almost drop into it from above, apparently without troubling itself about any preliminary examination. The bumble bees too are less fastidious in their closer inspection.

Many instances are recorded which illustrate the habit of bees to profit by previous successful or unsuccessful experiences. A sort of memory by association is developed so that older, more experienced bees often appear to work among blossoms to much better advantage than younger bees. As an illustration of the influence of previous association upon subsequent behavior, the writer cites the following interesting instance which has come under his observation at Thompson's Mills, North Georgia. It has been mentioned that the common honey bee sooner or later discovers the outer involucral nectaries of cotton blossoms and visits them very constantly, seemingly in preference to the inner floral

nectaries. These particular nectaries, although present in our common American cottons, are never found on the Asiatic cottons, *Hawasaki,* etc. In the writer's variety tests these foreign cottons have been grown side by side and sometimes intermingled in the rows with the American cottons. The honey bees, in passing from blossom to blossom, visiting each time the outer involucral nectaries occasionally met the Asiatic variety. The previous association with the American cottons and their outer involucral nectaries led these bees to visit without success similar structures of the unfamiliar Asiatic variety. The bees quickly recognized their error after alighting and left the blossoms. Is this procedure other than the working of an associative memory? The writer is of the opinion that the honey bees do not discover these extra-floral nectaries until after more or less association with cotton blossoms each summer. This habit of the honey bee appears to become more noticeable later in the season. During the season of 1908 it appeared to be very general. It is a habit which seems to be almost wholly confined to honey bees.

These visits of the bees to the outer basal portion of the Asiatic cotton blossoms indicate that the visual powers alone were employed throughout the process. Although the bees first discovered the blossoms by their conspicuous petals, it is evident that they were led to search for outer involucral nectaries on the Asiatic cotton blossoms solely by their familiarity with the general form and structure of cotton blossoms.

As an illustration of associative memory this behavior of the honey bees is exactly similar to the behavior of certain bees in experiments conducted by Pérez[4], who used scarlet pelargoniums which are not visited by bees, since those flowers possess no nectar. He added honey to certain flowers which were then visited by bees, and says:

[4] Pérez, J., "Notes Zoologiques" (*Actes de la Société Linnéenne de Bordeaux,* Vol. XLVII, série V, tome VII, pp. 250–251, 1894).

La couleur écarlate s'était si bien associée dans leur souvenir à l'idée du miel, qu'elles se passaient à la fin sur des fleurs de cette couleur n'en ayant pas reçu, et ne les quittaient qu' apres s'être assurées, par un examen scrupuleux et persistant, qu'elles n'avaient rien à y recueillir.

A translation of his own words follows: "Scarlet color and honey had become so closely associated in their minds that they finally alighted upon flowers of the same color which had received none, and would not leave until they had assured themselves by a scrupulous and persistent examination that these flowers had nothing to offer them." Plateau gets precisely the same results when he says:

Lorsque l'insecte avait ainsi absorbé le liquide d'un certain nombre defleurs miellees, il lui arrivait de se diriger vers les Pelargoniums non nunis de miel.[5]

"After the insects had gathered honey from a number of flowers to which it had been added, they were then led to visit Pelargonium blossoms which had not received it." These observations are hardly in agreement with the rather radical conclusions of Bethe[6] that bees are devoid of sense impressions, and are incapable of profiting by previous experiences, that their activities are purely reflex, mechanical. Forel, Wasman, Buttel-Reepen, Huber and others have shown, nevertheless, that bees do profit by previous experiences and form habits under certain conditions. Lovell[7] has shown that once bees have been accustomed to visiting a certain color, they tend to return to it regularly until it is to their advantage to change. Once the bees have entered the cotton fields, it is quite obvious that they are led to discover the blossoms by the conspicuous corolla. It would be interesting to learn just how they find the fields themselves. Although a single cotton blossom does not

[5] *Bulletin de l'Academie royale de Belgique*, 3e série, 33, January, 1897.

[6] Bethe Albrecht, "Durfen wir Ameisen und Beinen psychische Qualitäten zuschrieben?" in *Arch. f. d. ges. Physiologie*, Bd. 70, 1898.

[7] Lovell, John H., "The Color Sense of the Honey Bee: Can Bees Distinguish Colors?" AMER. NAT., Vol. XLIV, No. 527, November, 1910.

seem especially odoriferous, it is not improbable that a field of well-developed cotton plants may readily advertise its location to the olfactory sense of bees by odoriferous clouds, so to speak, which are wafted away with every air-movement. During a hot, sunny afternoon the combined odors volatilizing from the great numbers of foliage and floral nectaries, the pollen, etc., must be very considerable. Especially during clear sunny days following periods of cloudy or rainy weather bees become unusually active and numerous. Many of these visitors have no doubt learned the location of the fields by previous association.

THE DISTRIBUTION OF PURE LINE MEANS

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SEVERAL times recently we have been told that the means of a character in a series of pure lines form a "Quetelet's Curve."[1] Some of those responsible for this assertion seem to attribute a particular virtue to "Quetelet's Law," and to feel that the statement that the means of a series of pure lines form a chance curve furnishes uncontrovertible evidence for the genotype theory of heredity. The questions which interest the biologist are, first, whether the statement is true in the sense that it is made on a sufficient body of actual observations, and second, what is the general biological significance to be attached to it, if true.

But among these biologists the interpretation of the facts has apparently preceded the demonstration of the existence of the facts themselves. Now while it is not at all unlikely that the means of genotypes—if such entities in Johannsen's sense of the term do exist in nature—form a chance curve, it by no means follows that conversely a series of averages which can be arranged in a symmetrical variation polygon proves or even suggests the existence of differentiated pure lines or biotypes. Yet just such differences in means are being accepted and cited without criticism as valid evidence in support of Johannsen's sweeping generalizations.

A case in point is a paper by Roemer[2] on pure lines in peas. It is with regret that one criticizes Roemer's

[1] Compare, for example, in this connection: Nilsson-Ehle, *Bot. Not.*, 1907, pp. 113–140; Lang, *Zeitschr. f. Ind. Abst.- u. Vererbungsl.*, Vol. 4, pp. 15–16, 1910; Spillman, AMER. NAT., Vol. 44, p. 761, 1910; Pearl, AMER. NAT., Vol. 45, p. 423, 1911.

[2] Roemer, T., "Variabilitätsstudien," *Arch. f. Rassen- u. Gesellsch.-Biologie*, Vol. 7, pp. 397–469, 1910.

paper. It is an exceedingly laborious *Arbeit* and apparently done with scrupulous care. One who himself has experienced the labor of calculating a few tables of constants has sympathy for a worker who has industriously filled pages with them. But the tenability of the genotype theory is one of the most pressing of current evolutionary problems, and all available evidence must be scrutinized. Roemer's data are chosen for two very excellent reasons, the first of which is that of all of the men who have discussed the disposition of the means of pure lines in a "Quetelet's Curve," he is, so far as I am aware, the only one who has put on record sufficient data for a critical test of his conclusions. If without overtrying the case, as the lawyers have it, we can give the second reason, it is that Roemer's data and conclusions have been accepted as perfectly valid by genotype specialists. One of them, for example, says:

> The work is essentially a confirmation, with another plant, of Johannsen's epoch-making investigations on beans, though it lacks any extensive studies on the effect of selection within the pure line. The essential objective point of Roemer's research is rather to determine the biometric characteristics of pure lines as such in relation to the general population. Among the more important general results are the following:
>
> 1. The different biotypes in a population arrange themselves in frequency distributions in accord with Quetelet's Law.
>
> 2. No relation was found to exist between the variability of the biotypes (*i. e.*, variation within the general population) and variation within the pure lines.

Our problem is twofold. First, we have to determine whether Roemer is really justified in regarding his lines as differentiated. Second, we have to inquire concerning the critical value of his data as evidence in support of the genotype theory of heredity. Incidently we shall make the first of these problems serve as an illustration of the use of a coefficient of individual prepotency recently proposed in these pages.[3]

[3] Harris, J. Arthur, "A Coefficient of Individual Prepotency for Students of Heredity," AMER. NAT., Vol. 45, pp. 471–478. 1911.

II. THE PROBLEM OF DIFFERENTIATION IN ROEMER'S PURE LINES

The method of Roemer's study was very simple. In 1908 a population of pea plants was grown from a sample of ordinary seed. In 1909 the offspring of each of a number of these plants was studied separately, and the means of several characters calculated. By a comparison of selected pairs of these means Roemer concludes that the several lines differ from each other, and by a seriation of all the line means he obtains the Quetelet's curve.

Such evidence as this can not be accepted. Every mean calculated on a sample of individuals is more or less untrustworthy as a measure of the character in individuals in general, because of the errors of random sampling, and in attaching significance to a series of averages this fact must be fully taken into account. It can not adequately be allowed for by a comparison of selected cases with their probable errors.

First Test. A Comparison of the Variability within the "Pure Line" with that of the "Population"

One of the tests of the presence of differentiated "biotypes," "genotypes" or "pure lines" within a "population" is the comparison of the intra-line with the population variability. If both be the same there is no justification in the assumption that the population is composed of a number of differentiated pure lines.[4] If the variability of the population is greater than that of the individual lines it may (or may not) comprise a series of "genotypes."

The reason for this is obvious. The standard deviation within the pure line, σ, describes only the differences occurring among the individuals of the group, while Σ, the standard deviation of the group, includes also the amounts by which the several lines are differentiated.

[4] This is, of course, under condition that the individuals of the several pure lines are not reared under conditions which tend to increase artificially their variability beyond that of the population.

Roemer does not give us the population standard deviations for the several characters in 1909 but only the averages, m_1, m_2, m_3, $\cdots$, m_s, and the standard deviations σ_1, σ_2, σ_3, $\cdots$, σ_s. We may approximate the desired constants very closely indeed[5] by the following method.

Let there be s samples or pure lines of n_1, n_2, n_3, $\cdots$, n_s individuals each, with means m_1, m_2, m_3, $\cdots$, m_s, and standard deviations σ_1, σ_2, σ_3, $\cdots$, σ_s. These form the population $S(n) = N$, for which the physical constants Σ and M are desired.

The mean is clearly $M = S(nm)/S(n)$.

In calculating the S.D. we may take the first two rough moments, ν_1', ν_2', about any point we please and adjust by the familiar formula $\sigma^2 = \mu_2 = \nu_2' - \nu_1'^2$. If the moments be taken about 0[6] $\nu_1' = M$, and it is at once clear that for the population

$$\Sigma = \sqrt{\frac{S[n(m^2 + \sigma^2)]}{S(n)} - \left(\frac{S(nm)}{S(n)}\right)^2},$$

when S indicates a summation for all groups or lines.[7]

The population constants have been calculated by these formulæ for all the characters of Roemer's two large series. He has given population constants, M and Σ, for the 1908 series, the parents of the 1909 plants.

The two are conveniently laid side by side for comparison in Table I.[8] The data in hand hardly seem to justify detailed comparison with reference to probable

[5] There is no approximation in the formula. The accuracy in practise depends solely upon the trustworthiness of the original m's and σ's, and upon the number of decimal places retained in the arithmetical routine.

[6] For several advantages in doing this see AMER. NAT., Vol. 44, pp. 693–699. 1910.

[7] The application of the formula to Roemer's data is of course exceedingly laborious, involving as it does the determination and summation by pairs of 3,108 squares, and the summation of the products of their totals by the frequencies upon which they are based. The publication of a little tabulated data would have reduced many days' labor necessary for a critical test of his results to a few hours.

[8] The constants for 1908 are taken from Roemer's Table I. Those for 1909 are calculated by the formulæ given above.

errors. It will be noted at once that for all the characters the mean is higher in 1909[9]—indeed for some characters in the "Kapital Erbse" it is almost double that found in 1908! With one exception the standard

TABLE I

COMPARISON OF PHYSICAL CONSTANTS FOR 1908 AND 1909 POPULATIONS

Character and Comparison	Averages		Standard Deviations		Coefficient of Variation	
	Gelbe Viktoria-Erbse	Svalöfs Kapital-Erbse	Gelbe Viktoria-Erbse	Svalöfs Kapital-Erbse	Gelbe Viktoria-Erbse	Svalöfs Kapital-Erbse
Weight of Plant						
1908 Population	13.09	7.99	4.250	2.815	32.47	35.23
1909 "	20.82	20.39	6.568	7.127	31.54	34.95
1909/1908 Ratio	1.59	2.55	1.545	2.531	.97	.99
Length of Stem						
1908 Population	114.96	78.96	12.985	12.575	11.30	15.95
1909 "	136.81	158.42	16.331	20.163	11.93	12.73
1909/1908 Ratio	1.19	2.01	1.257	1.603	1.06	.80
Thickness of Stem						
1908 Population	24.03	20.50	2.766	2.081	11.50	10.15
1909 "	25.20	24.05	2.390	2.933	9.48	12.19
1909/1908 Ratio	1.05	1.17	.864	1.409	.82	1.20
Number of Pods						
1908 Population	4.59	5.62	1.364	1.805	20.72	32.12
1909 "	6.48	11.54	1.987	4.263	30.66	36.95
1909/1908 Ratio	1.41	2.05	1.456	2.361	1.48	1.15
Weight of Pods						
1908 Population	9.71	5.76	3.192	2.184	32.80	37.95
1909 "	11.28	10.26	4.290	4.407	38.03	42.98
1909/1908 Ratio	1.16	1.78	1.343	2.017	1.16	1.13
Number of Seeds						
1908 Population	19.64	24.02	6.267	8.418	31.91	35.05
1909 "	26.60	45.11	9.162	18.633	34.44	41.31
1909/1908 Ratio	1.35	1.88	1.461	2.213	1.08	1.18
Weight of Seeds						
1908 Population	7.63	4.56	2.569	1.833	33.67	40.21
1909 "	8.56	7.26	3.511	3.376	40.99	46.49
1909/1908 Ratio	1.12	1.59	1.366	1.841	1.22	1.16

deviations in 1909 are higher than those in 1908. Mean and standard deviation are generally closely correlated, and this doubtless accounts for the greater variability of the 1909 series. Possibly, however, the 1909 plants

[9] Roemer states that conditions for growth in 1909 were superior to those in 1908.

were grown under conditions more heterogeneous than those to which the 1908 plants were exposed. In the second case, the S.D. might be directly raised, *i. e.*, heterogeneity in the crop may be merely a reflection of heterogeneity in the substratum.

There is no way of determining whether Roemer's cultural conditions were more heterogeneous in 1909 than in 1908, but it must be noted that *in ten of the fourteen cases* the coefficient of variation is higher in 1909.

Two ratios are to be examined,

$$\frac{\text{Mean Pure Line Variability}}{\text{Parental Population Variability}}'$$

$$\frac{\text{Mean Pure Line Variability}}{\text{General Population Variability}}.$$

Consider first the ratio of the mean pure line to the parental population variability. If the offspring of the individual parents are differentiated we should expect to find the mean variability of the pure lines less than that of the parent population, providing, of course, that innate tendencies are not obscured by environmental factors. Table II[10] gives the necessary data.

Now the remarkable thing about these standard deviations is that in the most cases the variability within the individual "pure lines" in 1909 is greater than that of a mixture of all the pure lines in 1908. The excess is very striking in several cases. Of the fourteen comparisons, thirteen show a higher variability within the pure line than in the population. For the "Viktoria"

[10] For 1908 the population Σ and C.V. are from Roemer's Table I. The 1909 population Σ and C.V. have been calculated by the formulæ given above. The mean pure line standard deviations have been taken from Roemer's Tables II–III. None of the constants have been rechecked, since the original data are not available. The mean value of 12.13 for thickness of stem in Table II is obviously a printer's slip for 2.13. The mean pure line coefficients of variation are from Roemer's Table X. These were not calculated by dividing the sum of the coefficients of variation of the individual pure lines by the number of lines, but by dividing the mean standard deviation of the pure lines by the mean average of the pure lines.

the average M.P.L./Parental ratio is 1.327 while for the "Kapital" it is 1.996. The "pure line" variability is thus from 30 to 100 per cent. in excess of that of the population.

TABLE II

COMPARISONS OF MEAN PURE LINE AND POPULATION VARIABILITY

Character and Comparison	1908–1909. Standard Deviations		1908–1909. Coefficient of Variation		1909–1909. Standard Deviations	
	Gelbe Viktoria-Erbse	Svalöfs Kapital-Erbse	Gelbe Viktoria-Erbse	Svalöfs Kapital-Erbse	Gelbe Viktoria-Erbse	Svalöfs Kapital-Erbse
Weight of Stem						
Population...	4.250	2.815	32.47	35.23	6.568	7.127
Mean Pure Line.....	5 .96	6.44	28.53	31.40	5.96	6.44
M.P.L./Pop. Ratio	1.402	2.288	.88	.89	.907	.904
Length of Stem						
Population.....	12.985	12.575	11.30	15.95	16.331	20.163
Mean Pure Line.....	13.80	15.98	10.05	10.05	13.80	15.98
M.P.L./Pop. Ratio.	1.063	1.271	.89	.63	.845	.792
Thickness of Stem						
Population...	2.766	2.081	11.50	10.15	2.390	2.933
Mean Pure Line.....	2.13	2.04	8.45	8.46	2.13	2.04
M.P.L./Pop. Ratio	.770	.980	.73	.83	.891	.696
Number of Pods						
Population.....	1.364	1.805	29 72	32.12	1.987	4.263
Mean Pure Line.	1.80	3.92	27.19	34.00	1.80	3.92
M.P L./Pop. Ratio	1.320	2.172	.91	1.06	.906	.920
Weight of Pods						
Population...	3.192	2.184	32.80	37.95	4.290	4.407
Mean Pure Line	3.80	3.95	33.84	38.50	3.80	3.95
M.P.L./Pop. Ratio	1.190	1.809	1.03	1.01	.885	.896
Number of Seeds						
Population	6.267	8.418	31.91	35.05	9.163	18.633
Mean Pure Line.	8 01	16.60	33.30	36.80	8.01	16.60
M.P.L./Pop. Ratio.	1.278	1.972	1.04	1.05	.874	.891
Weight of Seeds						
Population...	2.569	1.833	33.67	40.21	3.511	3.376
Mean Pure Line.....	3.17	3.04	37.05	41.90	3.17	3.04
M.P.L./Po p. Ratio.....	1.234	1.658	1.10	1.04	.903	.900

The explanation of this anomalous result is first to be sought in the higher means (with the associated higher variability) in the 1909 plants. Basing the comparison on the coefficients of variation in order to eliminate, in so far as possible, the influence of the means, we note that seven of the ratios are greater and seven

are less than unity, while for all the mean is .936. On an average, therefore, the pure lines have 93.6 per cent. as much variability as the population.

The second comparison, that between the variability of the individual pure lines and the population which they form, can be made on the basis of the standard deviations alone since the means are the same. This comparison (the last two columns of Table II) shows that in both series and for every character the variability written, the line is less than that for the population. The lowest ratio is .70, the highest is .92 and the mean is .858. This test indicates that they are differentiated. This is, of course, the conclusion which Roemer drew from his selected individual comparisons.

Second Test. The Deviation of the Pure Line Means from the Population Mean

For characters measurable on a quantitative scale the test for the deviation of the offspring of an individual from its population is given by

$$(m - M) \pm .67449 \sqrt{\frac{\Sigma^2}{N} + \frac{\sigma^2}{n}\left(1 - \frac{2n}{N}\right) - \frac{n(M-m)^2}{N(N-n)}}.$$

Where m and M, σ and Σ, n and N are the means, standard deviations, and numbers of individuals for the family and the population, respectively.[11]

For reasons which will be apparent to the reader later, the data which are given us do not justify calculations to a high degree of refinement.[12] We therefore approximate in every point possible.

The expressions

$$1 - \frac{2n}{n}, \quad \frac{n(M-m)^2}{N(N-n)}$$

[11] AMER. NAT., Vol. 45, pp. 471–478. 1911.

[12] Furthermore, I have serious misgivings that Roemer's lines comprise so few individuals each that the coefficient suggested must be used with caution. It is not needful to consider the point in greater detail here.

may be disregarded, since with such relatively low values of n as those of Roemer's data the first is practically unity, while the second is generally insignificant and may always be neglected, having a maximum value of *circa* .010, and in the majority of the cases falling far towards zero. The values of Σ^2/N are given in Table III. In practically every case the inclusion of Σ^2/N in

TABLE III

VALUES OF Σ^2/N

Character	Gelbe Viktoria Erbse	Svalöfs Kapital Erbse
1. Weight of plant	.0233	.0292
2. Length of stem	.1442	.9204
3. Thickness of stem	.0031	.0049
4. Number of pods	.0021	.0105
5. Weight of pods	.0100	.0112
6. Number of seeds	.0454	.1997
7. Weight of seeds	.0067	.0066

formula would change the end result only insignificantly, and since we are working roughly it may be omitted throughout.

We have thus reduced the formula to the fundamental term $\sqrt{\sigma^2/n}$. Fortunately for us, Roemer has not used the correct formula for the probable error of the mean but has given Johannsen's "Mittlerer Fehler," $\sigma/\sqrt{n} = \sqrt{\sigma^2/n}$. We now simply determine $m - M$[13] and $(m - M)/(\sigma/\sqrt{n})$ for each of his lines. Table IV gives the ratios.

Apparently there can be no question concerning the reality of differentiation in Roemer's lines. If the differences $(m - M)$ were due purely to random sampling from a homogeneous population, we should expect the

[13] This second test was carried out before the first, and so before the actual population means and variabilities were available. The means used were Roemer's means of pure line averages, as given in his Table IX. These would be the same as the population means if all the lines had the same n. As a matter of fact, the agreement is very close in all. In two cases only did I modify Roemer's means—changing number of pods from 6.6 to 6.5 and weight of pods from 11.2 to 11.3, in the "Gelbe Viktoria Erbse."

TABLE IV

Ratio of Deviation to Probable Error	Character[14] in Gelbe Viktoria Erbse							Character in Svalöfs Kapital Erbse						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
— 15.5 to — 14.5	—	—	—	—	—	—	—	—	1	—	—	—	—	—
— 14.5 to — 13.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—
— 13.5 to — 12.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—
— 12.5 to — 11.5	—	—	—	—	—	—	—	—	—	—	—	—	—	1
— 11.5 to — 10.5	—	—	—	—	—	—	—	—	1	—	—	—	—	—
— 10.5 to — 9.5	—	—	—	—	—	—	—	—	1	—	—	—	—	—
— 9.5 to — 8.5	—	—	—	—	—	—	—	—	1	—	—	—	—	—
— 8.5 to — 7.5	—	—	—	—	—	—	—	—	—	—	1	—	—	—
— 7.5 to — 6.5	—	2	—	—	—	—	—	—	—	—	—	1	—	1
— 6.5 to — 5.5	—	—	—	1	1	—	—	—	1	—	1	—	1	—
— 5.5 to — 4.5	4	3	—	—	3	3	2	2	1	1	2	—	1	1
— 4.5 to — 3.5	1	5	3	4	1	4	4	5	6	2	5	5	2	3
— 3.5 to — 2.5	6	12	8	5	4	3	5	7	2	2	1	4	4	6
— 2.5 to — 1.5	13	12	18	13	15	18	14	8	8	15	7	10	11	13
— 1.5 to — 0.5	29	19	19	24	24	25	25	19	15	25	15	24	19	16
— 0.5 to + 0.5	24	13	29	31	28	22	24	26	18	30	36	17	22	19
+ 0.5 to + 1.5	25	21	13	23	22	24	23	26	25	12	21	28	27	30
+ 1.5 to + 2.5	8	14	10	9	9	13	12	9	13	13	12	14	15	12
+ 2.5 to + 3.5	5	6	9	2	5	1	4	3	7	3	4	2	4	4
+ 3.5 to + 4.5	1	2	4	2	1	2	1	—	3	2	2	1	—	—
+ 4.5 to + 5.5	—	3	1	1	—	—	—	1	1	1	—	1	1	1
+ 5.5 to + 6.5	—	2	1	—	—	1	—	1	1	1	—	—	—	—
+ 6.5 to + 7.5	—	—	—	—	—	—	—	—	1	—	—	—	—	—
+ 7.5 to + 8.5	—	1	—	—	1	—	1	—	1	—	—	—	—	—
+ 8.5 to + 9.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—
+ 9.5 to + 10.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—
+ 10.5 to + 11.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—
+ 11.5 to + 12.5	—	—	—	—	1	—	—	—	—	—	—	—	—	—

ratios $(m - M)/\sigma_{(m-M)}$ to have a standard deviation of $1 \pm .67449/\sqrt{2s}$, where s is the number of lines involved. The constants are given in Table V.

TABLE V

Character	Gelbe Viktoria Erbse	Svalöfs Kapital Erbse
1. Weight of plant	1.738 ± .077	1.886 ± .087
2. Length of stem	2.620 ± .117	3.209 ± .148
3. Thickness of stem	2.008 ± .089	1.768 ± .082
4. Number of pods	1.717 ± .076	1.955 ± .090
5. Weight of pods	2.213 ± .098	1.839 ± .085
6. Number of seeds	1.857 ± .083	1.759 ± .081
7. Weight of seeds	1.895 ± .084	2.188 ± .101

Now we remember that Roemer's individual lines are represented by so few individuals that our formula may not give absolutely trustworthy results, and that in case

[14] Numbers of characters are the same as in Tables III and V.

it does not, the discrepancy is in favor of the pure linist. But comparing these values with $1.000 \pm .044$ for "Viktoria" and $1.000 \pm .046$ for "Kapital," I think we must admit that the evidence is strongly in favor of a differentiation in these lines of peas.

III. The Bearing of These Data upon the Genotype Theory of Heredity

To the conclusion that these pure lines of peas are differentiated among themselves and that speaking roughly their means "form a Quetelet's Curve," there can be no objection, although this conclusion is by no means justified by Roemer's own analysis of his data. The assumption that these facts lend any support whatever to the genotype theory[15] seems to me to rest not only upon the most slipshod reasoning, but upon a complete disregard of simple biological precautions.

The chief of the pertinent reasons follow.

First. *There is no Evidence of Line or Genotypic Constancy or Heredity.*

By definition the genotype is a rigid organic entity, distinguished by breeding true from generation to generation, with the exception of mutations which are completely inherited and fluctuations which are not inherited at all. The mean of the line remains the same from generation to generation (except for rises and falls due to periodic environmental changes); the variations around these means are absolutely incapable of inheritance.

Roemer and his supporters of course assume this to be true for the *Pisum* series dealt with, but no fragment of evidence is adduced to show either (*a*) that these means remain the same from generation to generation, or (*b*) that selection within the pure line is ineffective. The condition is even worse than this. Roemer measured the

[15] The cardinal points of the genotype theory have been tersely, and I believe fairly, summarized elsewhere in these pages. See AMER. NAT., Vol. 45, pp. 346–363, 1911.

characters of the parent plants which furnished the seed from which his various pure lines were grown, but he neither determines whether there is any parental correlation in the population nor gives us the data from which this might be determined. To be sure, one may determine from his data that the variability within the individual line is less than that of the population, but this might be as easily attributed to the much-scouted "Galton's Law" as to genotypic heredity; possibly it is to be referred to some factor quite outside inheritance.[16] In fine, it is impossible to determine anything at all about inheritance from Roemer's data.

Second. *The Possibility of Environmental Heterogeneity is not Adequately Taken into Account.*

One of the first precautions of the experimental breeder should be to make sure that the environmental conditions to which his materials are subjected are not so heterogeneous as to vitiate entirely any conclusions concerning innate factors. Two watch glasses of *Paramecia* may present highly different environmental conditions. Food and housing are important factors in the egg records of poultry. Peas differ from row to row, or within the row, because of slight differences in the substratum. But experimenters now-a-days are so obsessed with the idea of rigid "unit characters," "determiners" and "genes" that little attention is paid to environmental influences; they are so absorbed in "analyzing" the "germ plasm" that they forget to make proper allowance for factors which may so modify the soma—which is the only available index of the germ plasm of an individual—that it is misleading as a guide to hereditary tendencies.

From my own experience in experimental cultures it seems quite possible that the differences in Roemer's lines are due to lack of uniformity in the substratum. One is

[16] For instance, de Vries has several times suggested that the feeding of the parent plant may have an effect on the offspring. I personally do not believe that this could be a sensible source of differentiation in Roemer's peas, but it is one of the factors which should be taken into account by a critical student of the problem.

not much impressed with the consistency of his results. Not only are his means and standard deviations much higher in 1909 than in 1908, but the relative variabilities are also higher in ten out of fourteen cases. To be sure, he has used the conventional precautions. He describes his field as a "gleichmässiger humoser Lehmboden," and states that the fertilizer was mixed with soil before application and distributed as evenly as possible. But for an organism so responsive to environmental influences as the garden pea,[17] and in a problem of this delicacy, these precautions are not at all sufficient. It is quite clear[18] that the seeds from each parent were planted together in rows, and if the soil differed at all from one part of the field to another the tendency would be for this heterogeneity to induce a differentiation in the crop.

If it be urged that we do not *know* that the differentiation in Roemer's means are due to environmental heterogeneity, the reply is simple. It is the duty of those who claim genotypic rank for observed differences to prove that their results are not due merely to faulty experimental conditions.

Third. *One or Both of Roemer's "Populations" are in Reality "Pure Lines."*

By definition a pure line is the offspring of a single individual of a continually self-fertilizing or vegetatively propagating organism. They may or may not be differentiated. Genotypists assume that generally they are both differentiated and highly constant. Selection within the line is absolutely incapable of effecting any change.

Now the curious thing about Roemer's material is that at least one, and possibly both, of the two populations suitable for our examination are in reality pure lines. Whether the "Individualauslese" by which the "Gelbe Viktoria Erbse" was developed gave rise to a pure line depends largely upon the stringency with which it was

[17] Roemer observes that the pea is exceedingly susceptible to environmental influences.

[18] See Roemer, *l. c.*, pp. 404–405.

carried out. Concerning "Svalöfs Kapital Erbse" there can be no doubt. The original plant was selected at Svalöf in 1896. Whether a further selection within the offspring of this plant was made, Roemer was unable to determine, but of the ancestry of his seed he felt quite certain.

Truly this is an anomalous state of affairs! Analyzed by the best available statistical methods, Roemer's data certainly indicate that the lines studied are significantly differentiated. Pure-line specialists dispense with any statistical analysis at all and accept the data as "a confirmation . . . of Johannsen's epoch-making investigations on beans." Yet if the differentiation in these lines be due to anything other than faulty experimental conditions, the observations described destroy entirely the value of Johannsen's theory by showing that heritable variations may occur in great numbers in the pure line.

IV. Summary and Conclusions

1. The statement that the means of the pure lines of a population form a "Quetelet's Curve" is now being made by genotypists. If it is true that an apparently homogeneous population is composed of a large number of slightly differentiated genotypes, it seems *a priori* not unlikely that their means will be arranged according to "Quetelet's Law." The question which concerns the biologist is whether this is, as a matter of fact, the condition found in nature. The object of the present rather laborious study has been to test the validity of this assertion on the basis of available facts. Roemer's data for pure lines in peas are the only passably satisfactory published series available.

2. Such a problem has two phases. It is first necessary to determine by adequate statistical tests that the lines in question may be reasonably regarded as differentiated biologically—*i. e.*, that the differences between them cannot be explained as the errors of random sampling, such

as give one a low or a high hand at cards. It is then allowable to consider the biological interpretation of the differences.

3. Two tests for differentiation were applied: (*a*) the mean intra-line variability was compared with the population variability, and (*b*) the significance of the deviation of individual line means from the population mean was tested by a coefficient of individual prepotency recently suggested. Both of these tests indicate sensible and statistically significant differences between the lines. These differences may be said to be distributed according to "Quetelet's Law" as the term is loosely used by biologists.

4. This fact *per se* furnishes no evidence at all for the genotypic nature of the differences in Roemer's lines. Indeed, throughout Roemer's work there is no conclusive evidence of any kind concerning any problem of heredity. At least one (and possibly both) of his series of material is from his own explicit statements in reality a pure line. The difference observed within these lines and considered by him and other pure linists to be of genotypic value and a confirmation of Johannsen's results with beans are probably merely the result of faulty experimental conditions. If they are not, Roemer's evidence goes squarely against Johannsen's theory.

COLD SPRING HARBOR, L. I.,
July 19, 1911.

SHORTER ARTICLES AND DISCUSSION

A SYSTEM OF RECORDING MENDELIAN OBSERVATIONS

In any experimental investigation the importance of making full, definite and at the same time simple and easily understood notes can hardly be overestimated. To record all pertinent observations in a convenient and easily accessible manner with the least expenditure of time and energy should be the object of the observer.

In connection with some investigations in plant breeding at the Massachusetts Experiment Station a system of records has been devised for use in experiments where segregation of characters occurs that has worked very well in practise and may be found suggestive to other observers who are investigating Mendelism and handling a considerable number of plants.

The records are kept on 5×8 index cards, though 4×6 cards might be preferred by some. All observations pertaining

BEAN. Variety CROSS 115 Series of 1907 Type, plant aj flower c Pod ak pr
leaf def fruit bs Seed g Plant 1-18

Plant, size Medium habit bush stem medium runners none
color Med. green season Med. Early bearing period short productiveness moderate
Leaves, size medium shape narrow color med green surface rough
petiole Blossom, color pink
Pods, length med.-long straightness nearly straight cross sect. oval color light green much splashed with purple
brittleness tough stringiness very stringy fibre much quality poor
disease sutures slight point medium
Pod Cluster, size medium position low depressions slight length
Seeds, number medium position crowded size (dry) 5 mm. length (dry) 11.5 mm
cross section oval ends truncate curvature slight color black
Notes

Experiment Department, Division of Horticulture, Massachusetts Agricultural College.

FIG. 1. Description Card.

to parent varieties or the F_1 generation are kept on blue cards and subsequent generations are recorded on buff, salmon and white cards. This provides for four generations which is about as many as are usually desired, but other colors are available if needed for subsequent generations. Four different blanks in each color are provided known as (1) description cards, (2) culture cards, (3) type cards and (4) blanks which are plain ruled cards used for miscellaneous notes. A description card applicable to beans is shown in Fig. 1. Cards suitable to other plants may, of course, be easily devised. These cards are not often used but are occasionally very convenient. Figure 2 shows a cul-

Crop Bean Hybrids Cross Series of 1910 Generation Crop of 1911

Planted May 17 1911 in 30 in. drills in plot 9 growth good

Transp. to no. plts. growth

Culture hand cultivated and hoed as necessary

Hybridization selfed, using cheese cloth bags.

Harvest Sept. 10.- 20 well matured, moderately productive

Notes

Plants grew slowly till July 1 when hot weather caused rapid growth. Pods setting at that time were short.

Experiment Department, Division of Horticulture, Massachusetts Agricultural College.

FIG. 2. Culture Card.

ture card that is used for any crop under observation and gives all necessary information concerning the care, cultivation and growth of any lot of plants.

The type card shown in Fig. 3 is the most important and distinctive feature of the system. A single line is given to each plant and furnishes opportunity for recording easily and quickly a wide range of observations. Each hybrid between parent varieties is given a serial number that is stamped at the top of the first column and beneath this are entered the numbers of the individual plants. Hybrids between different individuals of a variety are distinguished by the addition of a letter to this num-

ber which is discontinued when it appears that the plants are similar in constitution. Numbers given in each generation are carried along separated by a hyphen in the manner usually followed in such work.

Each character that appears is designated by a letter of the

CROSS 272 Plant	Plant Type	Leaf Type	Flower Type	Fruit Type	Pod Type	Seed Type	Notes SERIES OF 1910 CROP OF 1911
7-34	aj	b	c	as	bpv	gbo	
35			c	as	bpv	gbo	
36			c	as	ems	g	
37			b	bu	bpv	g	
38			b	bu	epv	dbo	
39			c	as	bms	dbo	
40			c	bu	bms	f	
41			c	bu	ems	gbo	
42			c	as	bpv	g	
43			b	as	bms	b	
44			c	as	epv	g	
8-1	aj	b	c	as	epv	g	
2			c	as	bpv	g	
3			c	as	bpv	gbo	
4			c	bu	bms	gbo	
5			c	bu	bpv	g	

Experiment Department, Division of Horticulture, Massachusetts Agricultural College.

FIG. 3. Type Card.

alphabet and in order to secure opportunity for recording a large number of characters they are more or less arbitrarily grouped, each group having if needed the whole twenty-six letters available. Each group is assigned a column in the card. In order to illustrate this a portion of the type designations we have used with beans is here given which with Fig. 3 will clearly show the application of the system. The same blank may of course be used with plants other than beans.

Plant type:
- *a* = stems green,
- *b* = stems with purple lines,
- *c* = stems purple tinged,
- *h* = pole form,
- *i* = runner form,
- *j* = bush form.

Flower types:
- *a* = white,
- *b* = light pink,

Fruit types:
- *a* = pod flat,
- *b* = pod oval,
- *e* = pod round,
- *s* = pod straight,
- *u* = pod curved.

Pod types:
- *a* = light green,
- *b* = medium green,
- *c* = dark green,

c = pink.

Leaf types:
a = light green,
b = medium green,
e = medium yellow,
h = broad,
i = medium.

m = no fiber,
p = much fiber,
s = stringless,
v = very stringy.

Seed types:
a = white,
b = buff,
c = yellow,
d = light red,
g = black,
m = medium eye,
o = dark mottling.

The notes shown in Fig. 3 give the following information: The cross in number 272 which is shown by a separate list and by a neighboring guide card to be Prolific Black Wax × Mohawk. This cross was one of those made in 1910 (Series 1910) and these plants were grown in 1911. (Crop of 1911.) The color of the card shows at once the generation. Plant 7–34 had green stems and was a bush bean. The leaf was medium green, the flower pink, the pod flat, straight, green, tough and stringy. The seed was black and buff mottled, the black predominating, as shown by *o* indicating dark mottling. All these observations are very quickly recorded, once they are determined and the record is brief, convenient, definite and easily summarized.

It is of course necessary to record clearly and positively just what is signified by each letter. Most characters appear in some established variety and may be fixed by referring to them. Full description or preserved material may supplement such references when necessary. Additional blank columns are provided to allow for more extended observations or they may be used in connection with the space to the right for brief special notes on the individual plant. If more extended notes regarding any plant or group of plants are desired, a description card or a blank card of the appropriate color may be inserted at any point for their accommodation. Photographs or drawings might also be easily filed if desirable.

We have used these cards for the past three years for recording observations on many thousands of plants, not only beans but several other kinds as well, and the system has given good satisfaction. If it contains any features useful to other observers the purpose of this article will be fulfilled.

J. K. SHAW.

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THE
AMERICAN NATURALIST

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THE INHERITANCE OF COLOR IN SHORTHORN CATTLE

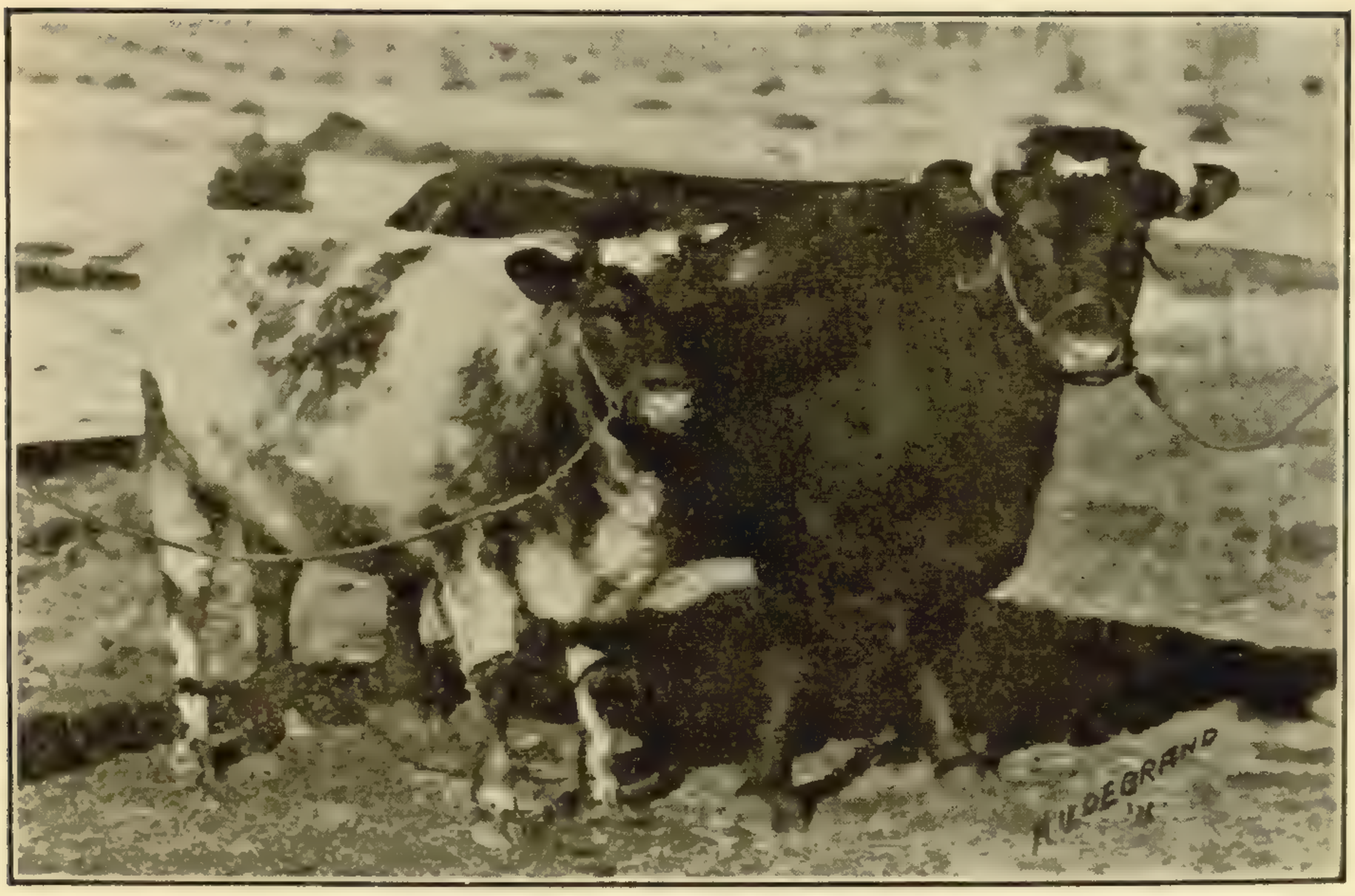
A STUDY IN SOMATIC BLENDS ACCOMPANYING GAMETIC SEGREGATION AND INTRA-ZYGOTIC INHIBITION AND REACTION

H. H. LAUGHLIN

CARNEGIE STATION FOR EXPERIMENTAL EVOLUTION,
COLD SPRING HARBOR, N. Y.

THE men who made the breed of Shorthorn cattle were in many respects the most skillful breeders of domestic animals. They had many rich and varied inheritance lines to draw upon, and in developing the breed they had high ideals of real excellence, largely ignoring the superficial quality of color. A consequence of this neglect of color is that the great breed of Shorthorn cattle is mongrel in this respect, ranging as follows: Solid red—varying from the richest dark to a light yellowish; spotted red-and-white; red-roan; and white—besides many intergrades and combinations of these shades and patterns. It is the prevailing experience among Shorthorn breeders that the color of the calf can not be accurately predicted before its birth. Reflecting this experience, Mr. B. O. Cowan, of the American Shorthorn Breeders' Association, writes:

> Owing to the fact that Shorthorns are of mixed colors, you can not with absolute certainty, before birth, tell what will be the color of the



Cinderella and Calf.

Mautalini 17th and Calf.

Pleasant Valley Bud and Calf.

Courtesy of Thos. Stanton, Wheaton, Ill.

COW—CINDERELLA. ***Red.*** (White star on forehead.)

Dam—Clara. ***Red.***
Dam's Dam—Carrie. ***Red.***
Dam's Sire—Prince Gloster. *Red.*
Sire—Scottish Minstrel. *Dark Roan.*
Sire's Dam—Imp. Mistletoe 20th. *Roan.*
Sire's Sire—Imp. Collynie Mint. *Roan.*

CALF—CINDERELLA 2D. ***Roan.***

Dam—Cinderella. ***Red.***
Dam's Dam—Clara. ***Red.***
Dam's Sire—Scottish Minstrel. *Dark Roan.*
Sire—Prince Imperial. *Light Roan.*
Sire's Dam—Imp. Helen 21st. *Light Roan.*
Sire's Sire—Prince. *Red.*

Courtesy of Geo. M. Rommel, Bureau of Animal Industry, Washington, D. C.

COW—MAUTALINI 17TH. ***Roan.*** (A champion Argentine (S. A.) cow.)

Dam—Mautalini 8th. *Red.*
Dam's Dam—Mautalini 3d. *Red.*
Dam's Sire—Farrier. *Roan.*
Sire—Conqueror's Crown. *Roan.*
Sire's Dam—Missie 157. *Roan.*
Sire's Sire—Bapton Conqueror. *Roan.*

CALF. ***Roan.***

Dam—Mautalini 17th. *Roan.*
Dam's Dam—Mautalini 8th. *Red.*
Dam's Sire—Conqueror's Crown. *Roan.*
Sire—True Blue. *Red and White.*
Sire's Dam—Twin Princess 10th. *Red and White.*
Sire's Sire—Bapton Champion. *Roan.*

Courtesy of F. W. Harding, Waukesha, Wis.

COW—PLEASANT VALLEY BUD. ***Roan.***

Dam—Rosebud 11th. *Red.*
Dam's Dam—Rosedale. *Red.*
Dam's Sire—John Bruce. *Roan.*
Sire—Ben Lomond (Imp.). *Red.*
Sire's Dam—Beauty 13th. *Roan.*
Sire's Sire—Count St. Clair. *Roan.*

CALF. ***Red.***

Dam—Pleasant Valley Bud. *Roan.*
Dam's Dam—Rosebud 11th. *Red.*
Dam's Sire—Ben Lomond (Imp.). *Red.*
Sire—Waverley. *Roan.*
Sire's Dam—Valley Gem. *Red.*
Sire's Sire—Mildred's Royal. *Roan.*

FIG. 1.

calves. There are a great many instances of red cows bred to white bulls producing red calves, in some instances white calves, and in other instances roans. In some herds in the United States where the breeders have used nothing but red for thirty or forty years it is very rare that they have any calves excepting reds; but even among these occasionally a calf is dropped that is either a roan or a red with some white marks —this is the influence of the blood of ancestors many generations back.

Mr. Spangler, of Sullivan County, Mo., reports the following to the *Breeders' Gazette* of February 17, 1909:

> My bull is white, but his sire and dam are both roan. The results are as follows: Since September first there have been fifty-five calves dropped to his service, of these forty-one are roan, nine red, four red-and-white, and one white. Twenty-six are bulls and twenty-nine heifers. The cow that dropped the white calf is herself a roan . . . the rest of the cows are red.

Robert Bruce, of County Dublin, Ireland, tabulated the color matings and color progeny of Shorthorns bred by Amos Cruickshank[1] at Sittyton. This he reports to the *Breeders' Gazette* of November 25, 1908, as follows:

TABLE I

Color of Matings	Color of Offspring				
	Red	Rd. & Wh.	Roan	White	Total
Red mated with red	133	12	34	1	180
Red mated with red and white	31	11	6	0	48
Red mated with roan	278	25	265	0	568
Red mated with white	1	0	41	4	46
Red and white mated with red and white	0	2	0	1	3
Red and white mated with roan	22	22	40	2	86
Red and white mated with white	0	1	1	1	3
Roan mated with roan	56	10	183	60	309
Roan mated with white	0	0	12	12	24
White mated with white	0	0	1	2	3
	521	83	583	83	1,270

Professor E. N. Wentworth, of Ames, Ia., supplies the following tabulation from random pedigrees:

[1] Amos Cruickshank, of Sittyton (1808–1895), the most distinguished breeder of Shorthorns, and one of the most skillful breeders of domestic animals.

TABLE II

Offspring	Parentage	
127 whites	43	from white by white matings.
	1	from red by red matings.
	83	from roan by roan matings.
645 roans	207	from roan by roan matings.
	122	from red by roan matings.
	8	from red by red matings.
	172	from white by red and white matings.
	136	from red by red and white matings.
892 reds	81	from roan by roan matings.
	439	from red by red matings.
	52	from red by red and white matings.
	320	from red by roan matings.
Total 1,664 animals		

The following table (No. III) records some matings, selected almost at random from the Shorthorn Herd Book, detailing the color of dam, sire and offspring, the last animal of this table, the *roan* cow Dorothea (Vol. 45, p. 645), herself a roan from two red parents, produced six calves: The first a *roan* Trout Creek Beauty, by the *red-and-white* Klondike of Baltimore; the second the *red-and-white* Lord Strathearn by the *red* Strathearn Oakland; the third the *red* Dorothea's Knight by the *red* Red Knight; the fourth the *white* Bapton Favorite by the *roan* Bapton Ensign; the fifth the *roan* Dorothea Second by the *red* March King, and the sixth the *red-and-white* Dorothea Third by the *red* March King. It is interesting to note that one cow can produce calves of each color characteristic of the race.

In color pattern the red-and-white and the roan-and-white Shorthorns are quite similar to all other breeds of cattle possessing broken patterns—that is to say, there is a tendency toward a white belt at the front flank, a slightly more pronounced one at the rear flank and a white underline. It is known that Angus cattle which are generally black sometimes possess white patches, generally within the line of the rear flank belt. A white Shorthorn bred to a black Angus or Galloway will produce a blue-roan calf, or when bred to a white-faced, roan-bodied

TABLE III

Dam			Sire			Offspring	
Grenedine	*White*	×	Wild Eyes	*Roan*	=	Grenedine 2nd	*Roan*
Jordan	*White*	×	The Baron	*Red and White*	=	Jewess	*Roan*
Jordan	*White*	×	Maple 4th	*Roan*	=	Truey	*Roan*
Farnside	*Roan*	×	Phoebus	*Roan*	=	Nuthall Prince	*White*
Farnside	*Roan*	×	Jeweller	*Roan*	=	Fair Maid	*Roan*
Farnside	*Roan*	×	Jeweller	*Roan*	=	Crown Prince	*Roan*
Farnside	*Roan*	×	Prince	*Roan*	=	Fanny Fern	*Roan*
Fawn	*Red and White*	×	Sir A. Windsor	*Red*	=	Ferculus	*Red and White*
Fawn	*Red and White*	×	Sir A. Windsor	*Red*	=	Friar	*Roan*
Repose	*Red and White*	×	4th Kent Oxford	*Light Roan*	=	Knightly Oxford	*Red and White*
Repose	*Red and White*	×	Red Cross Knight	*Red*	=	Red Cross Knight's Repose	*Red and White*
Repose	*Red and White*	×	Red Cross Knight	*Red*	=	Ruby	*Red and White*
Susan Gwynne	*Roan*	×	Sir Samuel	*Roan*	=	Soral	*Red*
Susan Gwynne	*Roan*	×	Conqueror	*White*	=	Lady Gwynne (Twins)	*White*
						Lord Gwynne (Twins)	*Roan*
Susan Gwynne	*Roan*	×	First Fruit	*Roan*	=	Earl Gwynne	*Roan*
Galaxy	*White*	×	Esca	*Roan*	=	Gaiety	*White*
Bapton Pearl	*Roan*	×	Auguston	*Roan*	=	Bapton Diamond	*Roan*
Bapton Pearl	*Roan*	×	Bapton Sultan	*Roan*	=	White Hall Sultan	*White*
Augusta Countess	*White*	×	Bapton Javelin	*Red*	=	Auguston	*Roan*
Moon Daisy	*Roan*	×	Capt. of the Guard	*Red*	=	Bapton Sultan	*Roan*
Victoria-of-Hill Farm 5th	*Roan*	×	Lavender Lad	*Red*	=	Victoria-of-Hill Farm 8th	*Roan*
Victoria-of-Hill Farm 8th	*Roan*	×	Robin Adair	*Red*	=	Proud Robin	*Red and Roan*
Victoria-of-Hill Farm 8th	*Roan*	×	Robin Adair	*Red*	=	White Hall Victor	*Red*
Victoria-of-Hill Farm 8th	*Roan*	×	White Hall Sultan	*White*	=	Glen Brook Sultan	*White*
Victoria-of-Hill Farm 8th	*Roan*	×	Victor Missie	*Red*	=	Victor Missie's Victoria	*Roan*
Sousie's Maid	*Roan*	×	Sheriff Hutton	*Roan*	=	Lady Jane Hutton	*Red*
Lady Jane Hutton	*Red*	×	Crimson Chief	*Red*	=	Dorothea	*Roan*

Hereford will produce a white-faced, roan-bodied or red-bodied calf. It is also known that a black Angus bred to a white-faced, red-bodied Hereford will produce a calf with a white face and a black body. A roan Shorthorn

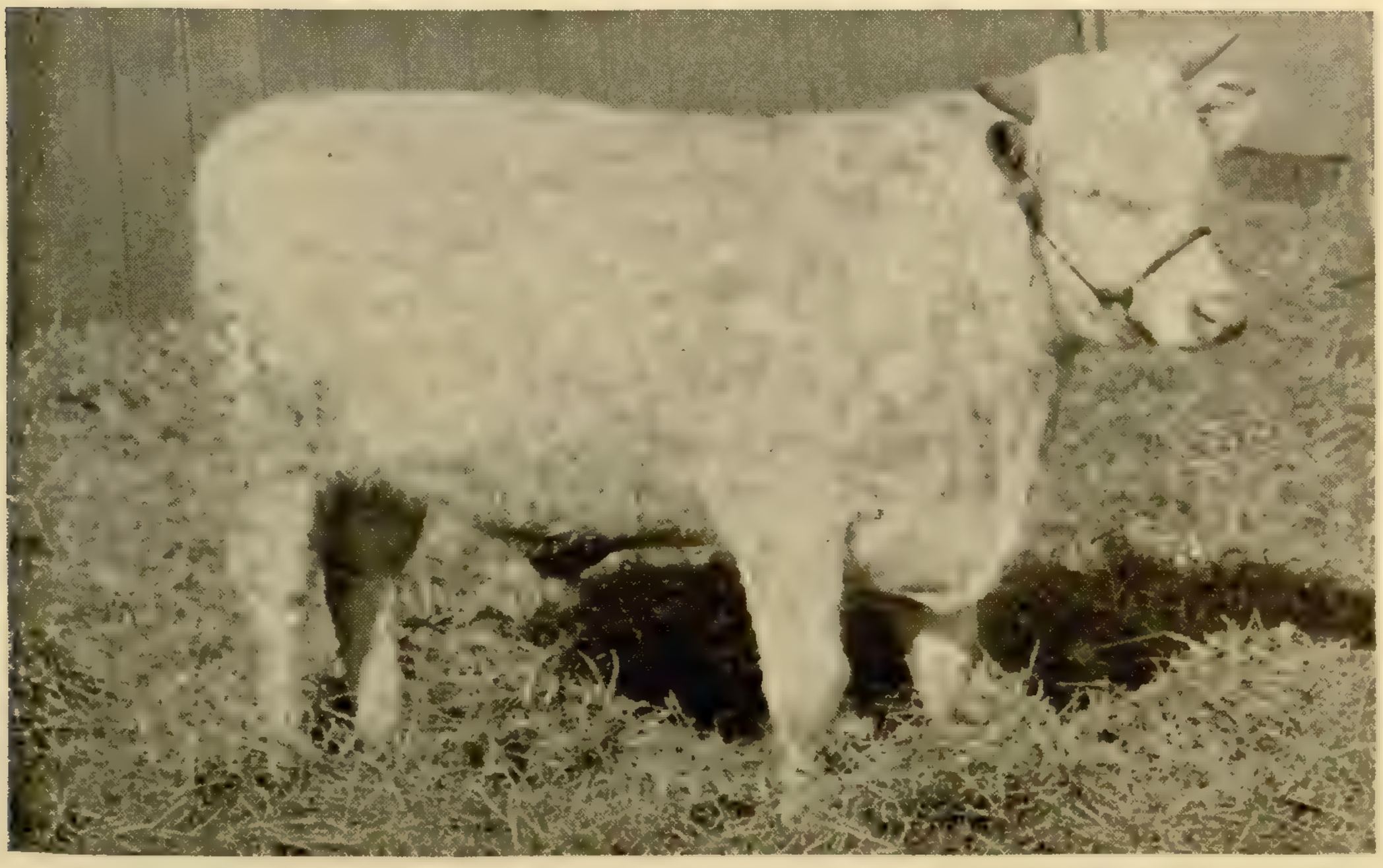


FIG. 2. BROODHOOKS CHIEF.

BROADHOOKS CHIEF 348176. *White.*

Courtesy of F. W. Harding, Waukesha, Wis.

Dam—Broadhooks Rose 101234. *Roan.*
Dam's Dam—Imp. Roan Rose 75966. *Roan.*
Dam's Sire—Rustic Chief 236800. *Roan.*

Sire—Royal Fancy 93217. *Roan.*
Sire's Dam—Sensation 7th. *Red.*
Sire's Sire—Prince of Fashion 64587. *Red.*

mated with a black Angus or Galloway will sometimes produce a black and sometimes a blue-roan calf; as instances of the former, Mr. Ralph B. Goodhue, of Donnelly, Minn., writes:

> I have had a few animals cross-bred between Angus and Shorthorn and in every instance have the offspring been black, sire and dams pure bred animals. I have bred 31/32 Holstein cows to red Shorthorn bulls and about 65 per cent. have been red-and-white, the rest being black-and-white, more black than white in markings. In breeding grade Shorthorn cows to pure bred Holstein bulls, have got black and white offspring. In the Hereford-Shorthorn, the red Shorthorn bred with the Hereford will most always give a mottled face on the offspring. The roan Shorthorn cows bred to Hereford bulls will give either a calf looking like a Hereford or a roan calf with clear white face.

Professor Wentworth, previously referred to, writes:

In regard to color coats in cattle hybrids, I can give you a few cases from my own experience.

We had three Holstein cows at home, two of them carrying a predominance of black, the other a predominance of white. As we had no Holstein bull on three successive years, they were bred to Shorthorn bulls. The first year when bred to a roan one of the calves came a blue gray. This calf was from the cow with the greatest amount of black. The others showed the pattern markings of their mothers. The second year they were bred to a deep red Shorthorn bull (all of the animals mentioned pure breds) and the color pattern showed no trace whatsoever of the Shorthorn parentage. The third year they were bred to a red and white bull. In the case of the lightest Holstein cow there seemed to be some tinge of red on the ends of the hair in the black pattern; however, at a distance it showed the same color.

I have seen Jersey-Holstein crosses usually partaking of the Holstein pattern with, perhaps, a slight admixture of dun color on the tips of the hair on the black markings.

I have seen Angus crossed on Jersey showing simply the black polled character, although in a few cases the extremities showed a slight tendency towards dun or fawn.

I have seen Angus crossed with Holstein and have seen both pure black and black-and-white cows. The instances which I have in mind are about twenty showing pure black and six or seven showing the black-and-white. However, these figures are simply a question of memory and might easily be modified. The case in question is that of a man with a Holstein herd who was forced to breed to an Angus bull one year.

Out at the dairy farm we have a Shorthorn cow, roan in color but a grade, which was bred to our Holstein bull, a half brother of Colanta 4th's Johanna. The calf is roan in color.

We also have some Arkansas backwoods cows; they are variegated in color pattern, showing red, dun, yellow, white, brindle and various other markings. A Holstein bull when bred to one of these produced a nearly pure black heifer. The black seemed to be rather tinged with brown at the ends of the hair, but the udder showed a white color. . . . A roan Shorthorn bull bred to a Hereford cow will quite frequently give a roan body with white Hereford markings. A red Shorthorn bull crossed with the Hereford cow is apt to increase the red splotches on the white markings of the Hereford.

Mr. P. G. Ross, of the famous Maxwalton Farm, Mansfield, O., relates his experience, throwing his observations into approximate percentages, as follows:

The color of the offspring of white Shorthorns depends largely on the ancestors, as about 50 per cent. of a bull's calves will have the color of

his dam and her ancestors. . . . We have used white on white and often had roan calves and in one instance had a red calf, but about 75 per cent. are white.

We have had considerable experience in crossing the Shorthorn on Angus. This we consider the best cross and the offspring is generally better than either of the parents. When crossing red and black the offspring are generally 75 per cent. blacks and even the second cross will not bring 50 per cent. reds; when crossing roan and black, about 50 per cent. will be blue-roans, 10 per cent. red-roans, 10 per cent. reds and 30 per cent. blacks. The Galloway color is much stronger than the Angus, consequently more dark calves will be expected. The Hereford cross is very strong as far as the white face is concerned and about 95 per cent. of white heads can be expected but the red of the body is easily blended into a roan and about 95 per cent. roan calves can be expected by a white bull, and at least 75 per cent. by roan bull, on Hereford cows.

The black of the Holstein seems to be particularly strong and when crossed with red the offspring will be nearly black and will remain very predominant to the third and fourth cross; the broken color shows itself but very little. . . . On the other hand, Holsteins take the roan color very readily and when crossed on white 95 per cent., and when crossed on roan 75 per cent. of the calves will be blue-roan. It is our experience that either the Holstein or the Hereford will take the roan color from a white or roan much oftener than from the red Shorthorn even if part of the red's ancestry were roans. The Red Polls and Devons seem to be very hard to blend into a roan and when crossed on a white not over 25 per cent. roans can be expected; the balance are red. This we do not consider strange as they have been bred red for so many generations. It would seem that the red color of the Shorthorn is not so strong as the roan when used in crossing, and in our opinion it is the most objectionable. . . . We believe that to maintain the standard we must exert judgment in crossing the best types and colors, as it is evident in both animals and plants that they must have fresh blood to prosper and this is seen much earlier in breeding the short-lived animals such as hogs, dogs, cats and rabbits. We feel that the Shorthorn has given a much better opportunity for crossing than any other breed of cattle as there is very little restriction as to standard color. The different color is, we feel, a very safe rule to go by in crossing and we are particularly opposed to using red on red no matter if the ancestors are desirable. We feel that white on red is the proper cross and roan is good to cross on anything.

The observed facts fit the following hypothesis so closely that it is presented as a further working basis in solving the problem of the prediction of the color and color pattern in Shorthorn cattle.

Hypothesis.—There are two groups of genetically independent sets of hairs intermingled to make up the Shorthorn color coat. One set is alternatively "positive white" (W) and red (R), in which the white is dominant and the red recessive; the other set is alternatively red (R) or "albinic white" (wr), in which the red is dominant and the white recessive. Dominant white is caused by a specific antibody existing in the zygote in small quantities, retarding or inhibiting the ontogenesis of the determiner for pigmentation. The same body existing in larger quantities reacts with and destroys the determiner for pigmentation, causing recessive or albinic white.

FIG. 3. ANOKA ACONITE 2D.

ANOKA ACONITE 2D 40311. *Roan.*

Courtesy of F. W. Harding, Waukesha, Wis.

Dam—Double Aconite 2d. Vol. 53, p. 563. *Red.*
Dam's Dam—Double Aconite. *Roan.*
Dam's Sire—Godoy 115575. *Red.*

Sire—Whitehall Marshall 209776. *Roan.*
Sire's Dam—Imp. Missie 167th. *Roan.*
Sire's Sire—Whitehall Sultan 163573. *White.*

The dominant white of the Shorthorn is doubtless derived from the Romano-British cattle, which it is generally conceded entered into the Shorthorn make-up, which element is to-day represented by the "Park Cattle." They

behave as dominant whites—*i. e.*, they themselves are white but sometimes throw red or black (not roan) calves. The recessive white doubtless came in with the Dutch flecked, the colored areas of which took the "differential coloring" because they lacked the positive graying factor; this recessive white must therefore be attributed to a strain of partial albinism. The spotted color pattern or coarse mosaic doubtless came in with the Dutch bulls of the eighteenth-century importation. The areas composing *Group One* are located about the two flank belts, the underline, the median line and the face and a fine network over the remainder of the body; those composing *Group Two* cover the neck, sides, back, hind quarters and legs in a network exclusive of the areas of Group One.

FACTORS CONSIDERED

W = Inhibitor of pigment formation.
w = Absence of such inhibitor.
R = Determiner for red pigmentation.
r = Absence of determiner for red pigmentation.

With reference to Set No. 1, or group-unit No. 1, individual cattle are gametically W_2r_2, W_wR_2 or w_2R_2. With reference to group-unit No. 2 they are w_2R_2, w_2R_r or w_2r_2. There are therefore involving these characters nine gametic and three somatic types of individuals, which types are set forth in the following table:

TABLE IV

	GAMETIC COMPOSITION Set 1	Set 2	Somatic Aspect	Blood	UNIT PURITY Set 1	Set 2
1	w_2R_2	w_2R_2	Red	Pure	Duplex	Duplex
2	w_2R_2	w_2Rr	Red	Mongrel	Duplex	Simplex
3	w_2R_2	w_2r_2	Roan	Pure	Duplex	Nulliplex
4	WwR_2	w_2R_2	Roan	Mongrel	Simplex	Duplex
5	WwR_2	w_2Rr	Roan	Mongrel	Simplex	Simplex
6	WwR_2	w_2r_2	White	Mongrel	Simplex	Nulliplex
7	W_2r_2	w_2R_2	Roan	Pure	Duplex	Duplex
8	W_2r_2	w_2Rr	Roan	Mongrel	Duplex	Simplex
9	W_2r_2	w_2r_2	White	Pure	Duplex	Nulliplex

Roan in this table stands for any animal with red and white hairs interspersed, regardless of the proportion or pattern.

All of these theoretical types seem to occur except the roan of type 3, which phenomenon will be discussed further on in this paper.

With these nine theoretical types of individuals the following forty-five type matings are possible. (The numbers following the color designations refer to the above table describing the individuals somatically and gametically.)

These forty-five cases typify the behavior of two companion traits of opposing patency in their dominant phases, thus explaining the behavior of one type of apparent or somatic blend, which is in fact the resultant somatic effect of the lack of synchronism in the behavior of genetically independent units.

With these matings it is noted that the cases joined by an arrow (cases 8 and 9, 10 and 11, 13 and 14, 17 and 18, 19 and 20, 22 and 23, 32 and 33, 34 and 35, and 37 and 38) are reciprocal cases wherein the same parental elements enter and the same offspring are expected, but these parental elements are differently combined in each pair of parents—different somatic but identical gametic matings. These principles fit the previously observed facts as follows: As to the attempt to establish a race of Red Shorthorns, the above mating No. 30 (a red by red) expects 25 per cent. roan offspring and amply accounts for the occurrence of roans in such a cross. This phenomenon is equally well accounted for by the simple hypothesis that red is dominant; some reds are simplex. It is known that breeders in attempting to eliminate white, spotted and roan from their stock simply destroyed the "off color" calf—the genotypic germ plasm that produced it being continued in the herd. There are, however, reds which will produce only reds, as in matings Nos. 6 and 15.

Mr. Spangler's white bull was produced by two roan parents; such color is expected from such a mating in one fourth of the offspring of matings Nos. 25, 26, 37; in three sixteenths of No. 28 and in one half of No. 34. His whiteness is of either type 6 or type 9 and consequently

TABLE V

	One Parent	2d Parent	Intermediate Calculations	Gametic and Somatic Composition of Offspring
1.	Set 1. (W_2r_2)	(W_2r_2)	$= 4\ W_2r_2$	16 $W_2r_2w_2R_2$
	Set 2. (w_2R_2)	(w_2R_2)	$= 4\ w_2R_2$	
	Somatic effect Roan 7	Roan 7		Roan 7
2.	(W_2r_2)	(WwR_2)	$= 2\ W_2r_2 + 2\ WwR_2$	8 $W_2r_2w_2R_2$ + 8 $WwR_2w_2R_2$
	(w_2R_2)	(w_2R_2)	$= 4\ w_2R_2$	
	Roan 7	Roan 4		Roan 7 Roan 4
3.	(W_2r_2)	(w_2R_2)	$= 4\ WwR_2$	16 $WwR_2w_2R_2$
	(w_2R_2)	(w_2R_2)	$= 4\ w_2R_2$	
	Roan 7	Red 1		Roan 4
4.	(WwR_2)	(WwR_2)	$= W_2r_2 + 2\ WwR_2 + w_2R_2$	4 $W_2r_2w_2R_2$ + 8 $WwR_2w_2R_2$ + 4 $w_2R_2w_2R_2$
	(w_2R_2)	(w_2R_2)	$= 4\ w_2R_2$	
	Roan 4	Roan 4		Roan 7 Roan 4 Red 1
5.	(WwR_2)	(w_2R_2)	$= 2\ WwR_2 + 2\ w_2R_2$	8 $WwR_2w_2R_2$ + 8 $w_2R_2w_2R_2$
	(w_2R_2)	(w_2R_2)	$= 4\ w_2R_2$	
	Roan 4	Red 1		Roan 4 Red 1
6.	(w_2R_2)	(w_2R_2)	$= 4\ w_2R_2$	16 $w_2R_2w_2R_2$
	(w_2R_2)	(w_2R_2)	$= 4\ w_2R_2$	
	Red 1	Red 1		Red 1
7.	(W_2r_2)	(W_2r_2)	$= 4\ W_2r_2$	8 $W_2r_2w_2R_2$ + 8 $W_2r_2w_2Rr$
	(w_2R_2)	(w_2Rr)	$= 2\ w_2R_2 + 2\ w_2Rr$	
	Roan 7	Roan 8		Roan 7 Roan 8

TABLE V (*continued*)

	One Parent	2d Parent	Intermediate Calculations	Gametic and Somatic Composition of Offspring
8.	(W_2r_2)	(WwR_2)	$= 2\ W_2r_2 + 2\ Wwr_2$	$4\ W_2r_2w_2R_2 + 4\ W_2r_2w_2Rr + 4\ WwR_2w_2R_2 + 4\ WwR_2w_2Rr$
↕	(w_2R_2)	(w_2Rr)	$= 2\ w_2R_2 + 2\ w_2R_2$	Roan 7 Roan 8 Roan 4 Roan 5
	Roan 7	Roan 5		
9.	(WwR_2)	(W_2r_2)	$= 2\ W_2r_2 + 2\ WwR_2$	$4\ W_2r_2w_2R_2 + 4\ W_2r_2w_2R_2 + 4\ WwR_2w_2R_2 + 4\ WwR_2w_2Rr$
	(w_2R_2)	(w_2Rr)	$= 2\ w_2R_2 + 2\ w_2Rr$	Roan 7 Roan 8 Roan 4 Roan 5
	Roan 4	Roan 8		
10.	(W_2r_2)	(w_2R_2)	$= 4\ WwR_2$	$8\ WwR_2w_2R_2 + 8\ WwR_2w_2Rr$
↕	(w_2R_2)	(w_2Rr)	$= 2\ w_2R_2 + 2\ w_2Rr$	Roan 4 Roan 5
	Roan 7	Red 2		
11.	(w_2R_2)	(W_2r_2)	$= 4\ WwR_2$	$8\ WwR_2w_2R_2 + 8\ WwR_2w_2Rr$
	(w_2R_2)	(w_2Rr)	$= 2\ w_2R_2 + 2\ w_2Rr$	Roan 4 Roan 5
	Red 1	Roan 8		
12.	(WwR_2)	(WwR_2)	$= W_2r_2 + 2\ WwR_2 + w_2R_2$	$2\ W_2r_2w_2R_2 + 2\ W_2r_2w_2Rr + 4\ WwR_2w_2R_2 + 4\ WwR_2w_2Rr$
	(w_2R_2)	(w_2Rr)	$= 2\ w_2R_2 + 2\ w_2Rr$	Roan 7 Roan 8 Roan 4 Roan 5
	Roan 4	Roan 5		$+ 2\ w_2R_2w_2R_2 + 2\ w_2R_2w_2Rr$
				Red 1 Red 2
13.	(WwR_2)	(w_2R_2)	$= 2\ WwR_2 + 2\ w_2R_2$	$4\ WwR_2w_2R_2 + 4\ WwR_2w_2Rr + 4\ w_2R_2w_2R_2 + 4\ w_2R_2w_2Rr$
↕	(w_2R_2)	(w_2Rr)	$= 2\ w_2R_2 + 2\ w_2Rr$	Roan 4 Roan 5 Red 1 Red 2
	Roan 4	Red 2		
14.	(w_2R_2)	(WwR_2)	$= 2\ WwR_2 + 2\ w_2R_2$	$4\ WwR_2w_2R_2 + 4\ WwR_2w_2Rr + 4\ w_2R_2w_2R_2 + 4\ w_2R_2w_2Rr$
	(w_2R_2)	(w_2Rr)	$= 2\ w_2R_2 + 2\ w_2Rr$	Roan 4 Roan 5 Red 1 Red 2
	Red 1	Roan 5		
15.	(w_2R_2)	(w_2R_2)	$= 4\ w_2R_2$	$8\ w_2R_2w_2R_2 + 8\ w_2R_2w_2Rr$
	(w_2R_2)	(w_2Rr)	$= 2\ w_2R_2 + 2\ w_2Rr$	Red 1 Red 2
	Red 1	Red 2		

TABLE V (*continued*)

	One Parent	2d Parent	Intermediate Calculations	Gametic and Somatic Composition of Offspring
16.	(W_2r_2)	(W_2r_2)	$= 4\ W_2r_2$	16 $W_2r_2w_2Rr$
	(w_2R_2)	(w_2r_2)	$= 4\ w_2Rr$	Roan 8
	Roan 7	White 9		
17.	(W_2r_2)	(WwR_2)	$= 2\ W_2r_2 + 2\ WwR_2$	8 $W_2r_2w_2Rr$ + 8 WwR_2w_2Rr
↕	(w_2R_2)	(w_2r_2)	$= 4\ w_2Rr$	Roan 8 Roan 5
	Roan 7	White 6		
18.	(WwR_2)	(W_2r_2)	$= 2\ W_2r_2 + 2\ WwR_2$	8 $W_2r_2w_2Rr$ + 8 WwR_2w_2Rr
	(w_2R_2)	(w_2r_2)	$= 4\ w_2Rr$	Roan 8 Roan 5
	Roan 4	White 9		
19.	(W_2r_2)	(w_2R_2)	$= 4\ WwR_2$	16 WwR_2w_2Rr
↕	(w_2R_2)	(w_2r_2)	$= 4\ w_2Rr$	Roan 5
	Roan 7	Roan 3		
20.	(w_2R_2)	(W_2r_2)	$= 4\ WwR_2$	16 WwR_2w_2Rr
	(w_2R_2)	(w_2r_2)	$= 4\ w_2Rr$	Roan 5
	Red 1	White 9		
21.	(WwR_2)	(WwR_2)	$= W_2r_2 + 2\ WwR_2 + W_2R_2$	4 $W_2r_2w_2Rr$ + 8 WwR_2w_2Rr + 4 $w_2R_2w_2Rr$
	(w_2R_2)	(w_2r_2)	$= 4\ w_2Rr$	Roan 8 Roan 5 Red 2
	Roan 4	White 6		
22.	(WwR_2)	(w_2R_2)	$= 2\ WwR_2 + 2\ w_2R_2$	8 WwR_2w_2Rr + 8 $w_2R_2w_2Rr$
↕	(w_2R_2)	(w_2r_2)	$= 4\ w_2Rr$	Roan 5 Red 2
	Roan 4	Roan 3		
23.	(w_2R_2)	(WwR_2)	$= 2\ WwR_2 + 2\ w_2R_2$	8 WwR_2w_2Rr + 8 $w_2R_2w_2Rr$
	(w_2R_2)	(w_2r_2)	$= 2\ w_2Rr$	Roan 5 Red 2
	Red 1	White 6		

TABLE V (*continued*)

	One Parent	2d Parent	Intermediate Calculations	Gametic and Somatic Composition of Offspring
24.	(w_2R_2)	(w_2R_2)	$= 4\ w_2R_2$	16 $w_2R_2w_2Rr$
	(w_2R_2)	(w_2r_2)	$= 4\ w_2Rr$	Red 2
	Red 1	Roan 3		
25.	(W_2r_2)	(W_2r_2)	$= 4\ W_2r_2$	$4\ W_2r_2w_2R_2 + 8\ W_2r_2w_2Rr + 4\ W_2r_2w_2r_2$
	(w_2Rr)	(w_2Rr)	$= w_2R_2 + 2\ w_2Rr + w_2r_2$	Roan 7 Roan 8 White 9
	Roan 8	Roan 8		
26.	(W_2r_2)	(WwR_2)	$= 2\ W_2r_2 + 2\ WwR_2$	$2\ W_2r_2w_2R_2 + 4\ W_2r_2w_2Rr + 2\ W_2r_2w_2r_2 + 2\ WwR_2w_2R_2$
	(w_2Rr)	(w_2Rr)	$= w_2R_2 + 2\ w_2Rr + w_2r_2$	Roan 7 Roan 8 White 9 Roan 4
	Roan 8	Roan 5		$+ 4\ WwR_2w_2Rr + 2\ WwR_2w_2r_2$
				Roan 5 White 6
27.	(W_2r_2)	(w_2R_2)	$= 4\ WwR_2$	$4\ WwR_2w_2R_2 + 8\ WwR_2w_2Rr + 4\ WwR_2w_2r_2$
	(w_2Rr)	(w_2Rr)	$= w_2R_2 + 2\ w_2Rr + w_2r_2$	Roan 4 Roan 5 White 6
	Roan 8	Red 2		
28.	(WwR_2)	(WwR_2)	$= W_2r_2 + 2\ WwR_2 + w_2R_2$	$W_2r_2w_2R_2 + 2\ W_2r_2w_2Rr + W_2r_2w_2r_2 + 2\ WwR_2w_2R_2$
	(w_2Rr)	(w_2Rr)	$= w_2R_2 + 2\ w_2Rr + w_2r_2$	Roan 7 Roan 8 White 9 Roan 4
	Roan 5	Roan 5		$+ 2\ WwR_2w_2r_2 + w_2R_2w_2R_2 + 2\ w_2R_2w_2Rr + w_2R_2w_2r_2$
				White 6 Red 1 Red 2 Roan 3
				$+ 4\ WwR_2w_2Rr$
				Roan 5
29.	(WwR_2)	(w_2R_2)	$= 2\ WwR_2 + 2\ w_2R_2$	$2\ WwR_2w_2R_2 + 4\ WwR_2w_2Rr + 2\ WwR_2w_2r_2 + 2\ w_2R_2w_2R_2$
	(w_2Rr)	(w_2Rr)	$= w_2R_2 + 2\ w_2Rr + w_2r_2$	Roan 4 Roan 5 White 6 Red 1
	Roan 5	Red 2		$+ 4\ w_2R_2w_2Rr + 2\ w_2R_2w_2r_2$
				Red 2 Roan 3
30.	(w_2R_2)	(w_2R_2)	$= 4\ w_2R_2$	$4\ w_2R_2w_2R_2 + 8\ w_2R_2w_2Rr + 4\ w_2R_2w_2r_2$
	(w_2Rr)	(w_2Rr)	$= w_2R_2 + 2\ w_2Rr + w_2r_2$	Red 1 Red 2 Roan 3
	Red 2	Red 2		

TABLE V (*continued*)

	One Parent	2d Parent	Intermediate Calculations	Gametic and Somatic Composition of Offspring
31.	(W_2r_2)	(W_2r_2)	$= 4\ W_2r_2$	$8\ W_2r_2w_2Rr + 8\ W_2r_2w_2r_2$
	(w_2Rr)	(w_2r_2)	$= 2\ w_2Rr + 2\ w_2r_2$	Roan 8 White 9
	Roan 8	White 9		
32.	(W_2r_2)	(WwR_2)	$= 2\ W_2r_2 + 2\ WwR_2$	$4\ W_2r_2w_2Rr + 4\ W_2r_2w_2r_2 + 4\ WwR_2w_2Rr + 4\ WwR_2w_2r_2$
↑	(w_2Rr)	(w_2r_2)	$= 2\ w_2Rr + 2\ w_2r_2$	Roan 8 White 9 Roan 5 White 6
↓	Roan 8	White 6		
33.	(WwR_2)	(W_2r_2)	$= 2\ W_2r_2 + 2\ WwR_2$	$4\ W_2r_2w_2Rr + 4\ W_2r_2w_2r_2 + 4\ WwR_2w_2Rr + 4\ WwR_2w_2r_2$
	(w_2Rr)	(w_2r_2)	$= 2\ w_2Rr + 2\ w_2r_2$	Roan 8 White 9 Roan 5 White 6
	Roan 5	White 9		
34.	(W_2r_2)	(w_2R_2)	$= 4\ WwR_2$	$8\ WwR_2w_2Rr + 8\ WwR_2w_2r_2$
↑	(w_2Rr)	(w_2r_2)	$= 2\ w_2Rr + 2\ w_2r_2$	Roan 5 White 6
↓	Roan 8	Roan 3		
35.	(w_2R_2)	(W_2r_2)	$= 4\ WwR_2$	$8\ WwR_2w_2Rr + 8\ WwR_2w_2r_2$
	(w_2Rr)	(w_2r_2)	$= 2\ w_2Rr + 2\ w_2r_2$	Roan 5 White 6
	Red 2	White 9		
36.	(WwR_2)	(WwR_2)	$= W_2r_2 + 2\ WwR_2 + w_2R_2$	$2\ W_2r_2w_2Rr + 2\ W_2r_2w_2r_2 + 4\ WwR_2w_2Rr + 4\ WwR_2w_2r_2$
	(w_2Rr)	(w_2r_2)	$= 2\ w_2Rr + 2\ w_2r_2$	Roan 8 White 9 Roan 5 White 6
	Roan 5	White 6		$+ 2\ w_2R_2w_2Rr + 2\ w_2R_2w_2r_2$
				Red 2 Roan 3
37.	(WwR_2)	(w_2R_2)	$= 2\ WwR_2 + 2\ w_2R_2$	$4\ WwR_2w_2Rr + 4\ WwR_2w_2r_2 + 4\ w_2R_2w_2Rr + 4\ w_2R_2w_2r_2$
↑	(w_2Rr)	(w_2r_2)	$= 2\ w_2Rr + 2\ w_2r_2$	Roan 5 White 6 Red 2 Roan 3
↓	Roan 5	Roan 3		
38.	(w_2R_2)	(WwR_2)	$= 2\ WwR_2 + 2\ w_2R_2$	$4\ WwR_2w_2Rr + 4\ WwR_2w_2r_2 + 4\ w_2R_2w_2Rr + 4\ w_2R_2w_2r_2$
	(w_2Rr)	(w_2r_2)	$= 2\ w_2Rr + 2\ w_2r_2$	Roan 5 White 6 Red 2 Roan 3
	Red 2	White 6		

TABLE V (*continued*)

	One Parent	2d Parent	Intermediate Calculations	Gametic and Somatic Composition of Offspring
39.	(w_2R_2)	(w_2R_2)	$= 4\ w_2R_2$	$8\ w_2R_2w_2Rr + 8\ w_2R_2w_2r_2$
	(w_2Rr)	(w_2r_2)	$= 2\ w_2Rr + 2\ w_2r_2$	
	Red 2	Roan 3		Red 2 Roan 3
40.	(W_2r_2)	(W_2r_2)	$= 4\ W_2r_2$	$16\ W_2r_2w_2r_2$
	(w_2r_2)	(w_2r_2)	$= 4\ w_2r_2$	
	White 9	White 9		White 9
41.	(W_2r_2)	(WwR_2)	$= 2\ W_2r_2 + 2\ WwR_2$	$8\ W_2r_2w_2r_2 + 8\ WwR_2w_2r_2$
	(w_2r_2)	(w_2r_2)	$= 4\ w_2r_2$	
	White 9	White 6		White 9 White 6
42.	(W_2r_2)	(w_2R_2)	$= 4\ WwR_2$	$16\ WwR_2w_2r_2$
	(w_2r_2)	(w_2r_2)	$= 4\ w_2r_2$	
	White 9	Roan 3		White 6
43.	(WwR_2)	(WwR_2)	$= W_2r_2 + 2\ WwR_2 + w_2R_2$	$4\ W_2r_2w_2r_2 + 8\ WwR_2w_2r_2 + 4\ w_2R_2w_2r_2$
	(w_2r_2)	(w_2r_2)	$= 4\ w_2r_2$	
	White 6	White 6		White 9 White 6 Roan 3
44.	(WwR_2)	(w_2R_2)	$= 2\ WwR_2 + 2w_2R_2$	$8\ WwR_2w_2r_2 + 8\ w_2R_2w_2r_2$
	(w_2r_2)	(w_2r_2)	$= 4\ w_2r_2$	
	White 6	Roan 3		White 6 Roan 3
45.	(w_2R_2)	(w_2R_2)	$= 4\ w_2Rr$	$16\ w_2R_2w_2r_2$
	(w_2r_2)	(w_2r_2)	$= 4\ w_2r_2$	
	Roan 3	Roan 3		Roan 3

when mated with red cows only roan calves are expected if the mating be like mating No. 20; 50 per cent. red and 50 per cent. roan if like No. 23; 50 per cent. roan and 50 per cent. white if like No. 35; and 50 per cent. roan, 25 per cent. red and 25 per cent. white if like No. 38. There is ample explanation for throwing a white calf from a roan cow and a white bull. If the mating be like Nos. 31,

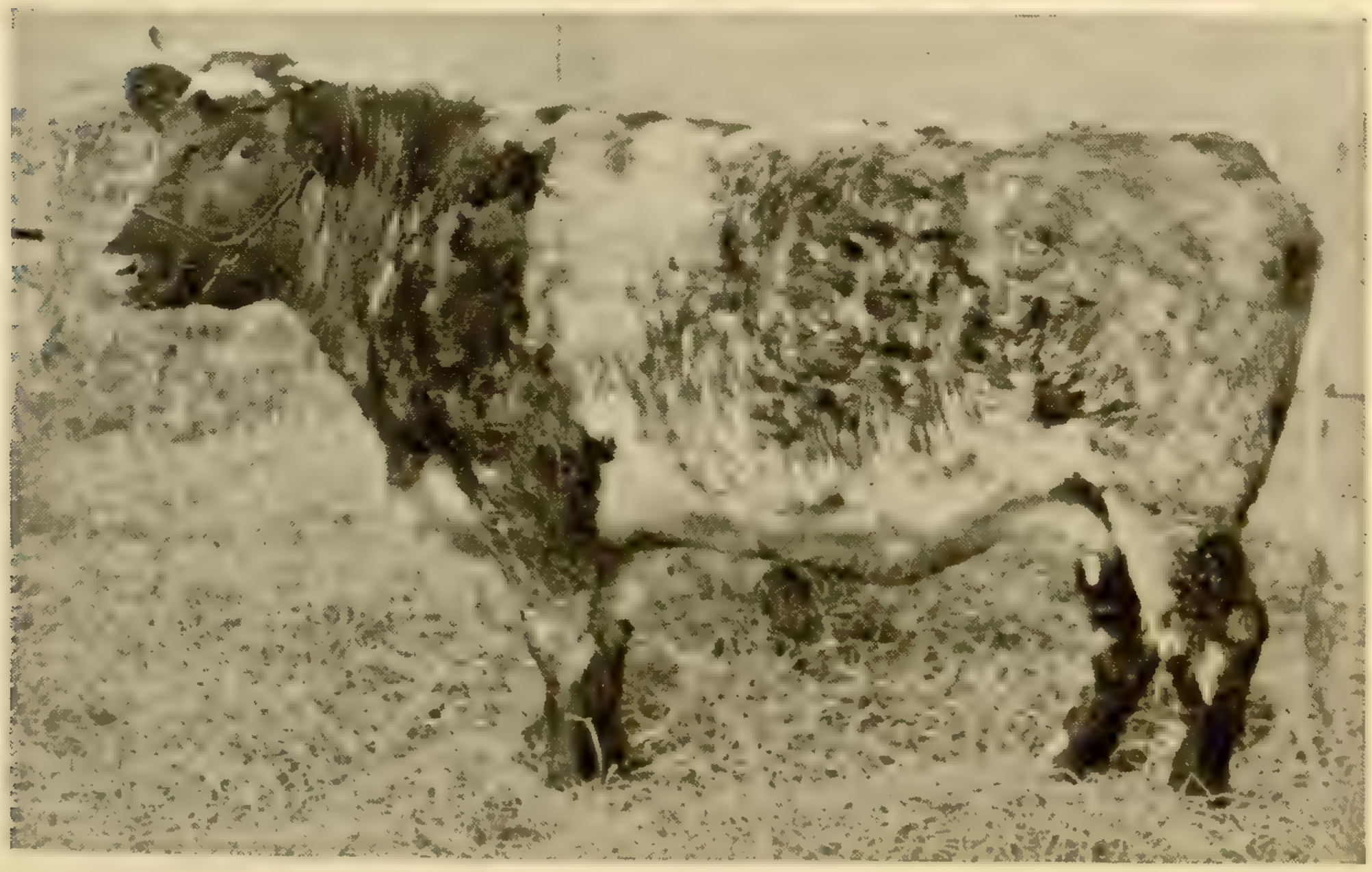


FIG. 4. FLORINDA SULTANA.

FLORINDA SULTANA 70519. *Roan.*

Courtesy of F. W. Harding, Waukesha, Wis.

Dam—Gertrude, Vol. 60, p. 1110. *Red.*
Dam's Dam—Wild Eye Belle 15th. *Red.*
Dam's Sire—Judge Wardell 144980. *Red.*

Sire—White Hall Sultan 163573. *White.*
Sire's Dam—Bapton Pearl. *Roan.*
Sire's Sire—Bapton Sultan 163570. *Roan.*

32, 33 or 44 the chance for roan and white colors are equal; if like No. 36 the ratio of white to roan to red expected is 6 to 8 to 2, but if the mating be of type 42 only white calves can be expected.

Mr. Bruce's array of data concerning the Sittyton cattle presents a very telling table of facts. All possible color matings are made, and in most cases the number of offspring is quite large enough to insure a proportional distribution among the expected colors. The facts of this table fit the hypothesis quite significantly. Of special

interest are the roan by roan matings, which produced 56 reds, 193 mixed color (*i. e.*, roan and red-and-white) and 60 white offspring. This does not fit well into the now abandoned hypothesis that "roans are simplex, reds are duplex and whites nulliplex." The number being quite large should approximate more nearly the expected 50 per cent. of roans, or even less than 50 per cent., inasmuch as some reds were later thought to be simplex; however, there are 62.46 per cent. roans. This may mean that some roans are pure and when mated to like animals will produce only roans—as mating No. 1, wherein two roans produce only roans, which in turn are pure and will reproduce themselves. As further explanation in accounting for an excess of roans—which is common in most herds—note that in matings Nos. 1, 2, 7, 8, 9, 19 and 45 a roan mated with a roan produces roans only. As to the red by red matings, types Nos. 6 and 15 will give only red offspring, while type 30 gives 75 per cent. red and 25 per cent. roan, which fits very well the distribution—133 red, 12 red-and-white, 34 roan and 1 white—with the exception of the one white which will be discussed a little further on. As a matter of fact, every possible color mating has been reported to throw every other color characteristic of the breed.

The red Shorthorn calf of white parentage is no doubt derived as follows: Save for occasional insignificant red patches in the ears, many Park Cattle are *solid* dominant white; this element in a few cattle of the Shorthorn breed would in the course of time, by the laws of chance, make the mating Sets 1 and 2 (WwR_2), Sets 1 and 2 (WwR_2), which would throw 25 per cent. red calves; this apparently is exactly what has happened. Moreover, the much more frequently possible white by white mating

$$\text{Sets 1 and 2 } (WwR_2) \left\{ \begin{array}{c} (WwR_2) \\ \text{Set 1} \\ (w_2r_2) \\ \text{Set 2} \end{array} \right\} \text{ will produce } 12\tfrac{1}{2} \text{ per cent. red offspring.}$$

The red-by-red mating that produces a white calf is

either of *very* rare occurrence or does not occur at all. Besides the cases just referred to, Pearson and Barrington[2] reported two Shorthorn matings reputed to have been red by red that produced white calves. Cases of such rarity and import should be supported by more painstakingly minute evidence than that offered by the

FIG. 5. SPICY SULTAN.

SPICY SULTAN 334972. *Roan.*

Courtesy of F. W. Harding, Waukesha, Wis.

Dam—Spicy of Edna, Vol. 50, p. 532. *Red, little White.*
Dam's Dam—Spicy of Browndale 9th. *Red.*
Dam's Sire—Orange Victor 138562. *Red.*

Sire—Whitehall Sultan 163573. *White.*
Sire's Dam—Bapton Pearl. *Roan.*
Sire's Sire—Bapton Sultan 163570. *Roan.*

herd book, which often records an animal as red though it may have white or roan areas of quite noticeable extent, or an animal as "white" that may have, besides the generally characteristic red in and about the ears, small body areas of red or of roan. Mr. E. M. Hall, a prominent Shorthorn breeder of Carthage, Missouri, in response to a recent inquiry, wrote: "I now, March 30, 1911, have one white calf—from red dam and sire, but it is an inbred calf." In response to further solicitation he

[2] "On the Inheritance of Coat-Colour in Cattle," *Biometrika,* 1905–6, p. 442.

kindly supplied the data for the following descriptive pedigree:

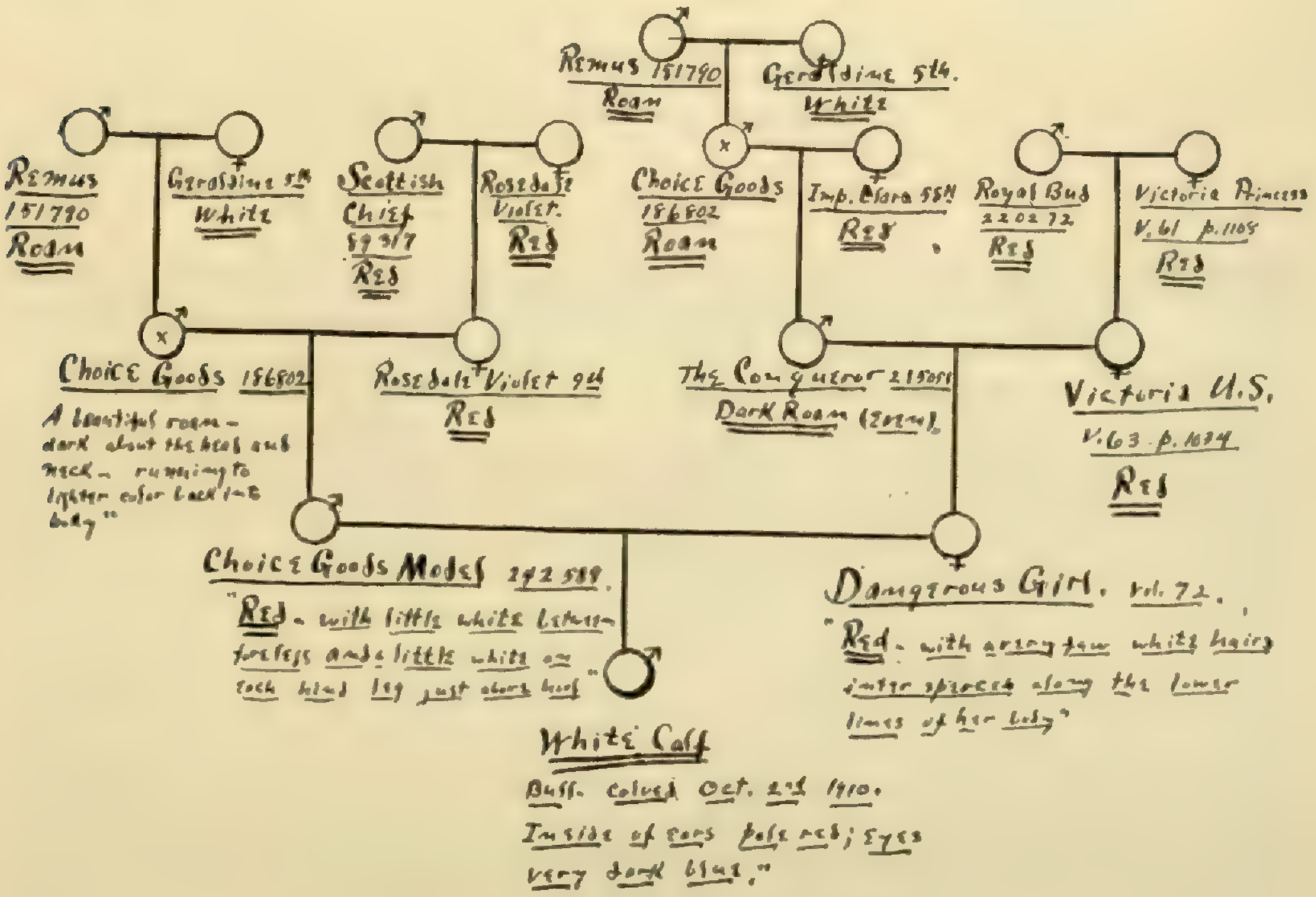


CHART I. Ancestry of White Calf.

Following the nomenclature of this paper this mating, because each parent had both red and white hairs, would be classed as "roan" by "roan" and the white calf could be accounted for easily; but the case should not be dismissed so summarily. There are red Shorthorns without a single white hair and, although red hair in and about the ear is quite persistent, there are *white* Shorthorns without a single red hair. If a mating of such red animals should have been known to have produced a *white* calf it might be accounted for on the grounds of mutation due to an intrusion *de novo* of an inhibitory or destroying antibody in quantity sufficient to affect the entire coat. As an alternative possibility, it might be that by chance the duplex red areas (w_2R_2) of one parent were in the homologous areas of the other simplex red (w_2R_r), a condition very remotely, if at all, possible on account of the absence of the reciprocally colored patterns in cattle. However, should it be possible, the process would be as follows:

	1st Parent	2d Parent		Offspring
Set 1.	(w_2R_2)	(w_2Rr)	$= 2\ w_2R_2 + 2\ w_2Rr$	$4\ w_2R_2w_2R_2$ (Red) $4\ w_2R_2w_2Rr$ (Red) $4\ w_2Rrw_2R_2$ (Red) $4\ w_2Rrw_2Rr$ (Red)
Set 2.	(w_2Rr)	(w_2R_2)	$= 2\ w_2R_2 + 2\ w_2Rr$	
	(Red)	(Red)		

Now mate two of the latter type—*w_2Rr w_2Rr*

			Offspring
(w_2Rr)	(w_2Rr)	$= w_2R_2 + 2\ w_2Rr + w_2r_2$	$w_2R_2w_2R_2$ (Red) $2\ w_2R_2w_2Rr$ (Red) $w_2R_2w_2r_2$ (Roan) $2\ w_2Rrw_2R_2$ (Red) $4\ w_2Rrw_2Rr$ (Red) $2\ w_2Rrw_2r_2$ (Roan) $w_2r_2w_2R_2$ (Roan) $2\ w_2r_2w_2Rr$ (Roan) $w_2r_2w_2r_2$ (*White*)
(w_2Rr)	(w_2Rr)	$= w_2R_2 + 2\ w_2Rr + w_2r_2$	

A white thus derived from two reds would be an albino as far as coat color is concerned. As still another possibility it may be that a strain albinic as to its entire coat entered into the Shorthorn make-up; this, while the simplest explanation, can not, however, be shown historically. While the areas of dominant white and albinic are quite specific, still, in view of the facts that the whitening process is systematically progressive and that the albinic condition is the more advanced, the areas of albinic white must ultimately encroach upon those of dominant white. Thus an animal whose coat is mostly albinic white, bred to a duplex red, would produce a simplex red (with little white), which latter animal could produce white offspring. This may be what sometimes happens. But again it involves the existence of a strain with an entire albinic coat. Thus the behavior in heredity of the pattern and pigments of the white calf belonging to Mr. Hall becomes of absorbing interest. If it should be retained as a herd bull and proves to be an animal of type No. 6 or No. 9, then the "roan-by-roan" theory or the intrusion de novo theory must be accepted; if, however, it will produce black calves when bred to an Angus or Galloway cow "the reciprocal areas" theory or the "albino" theory must be accepted. Present evidence seems to point toward the "roan-by-roan" theory and the impossibility of a mating of an absolutely red by an absolutely red producing any-

thing but red or roan calves—mutations excepted. In the present light, the absence of white calves from red parents, the absence of entire coat albinos, and the absence of theoretical type No. 3 are mutually corroborative phenomena. The fact that white by white—Table I—produced a roan may mean nothing more than that the mating was of type No. 43, in which 75 per cent. white and 25 per cent. roan offspring are expected.

As to the spotted animals, they seem to be of the same nature as the roans. Just as there are mulattos and "spotted" negroes due, respectively, to fine and coarse mosaics of the pigment granules, there are roan cattle, which roan effect is due to a very close intermingling of red and white hairs; and spotted cattle, due to a coarser mosaic of the same, which coarser mosaic came from a distinct inheritance source—doubtless the Dutch bulls of eighteenth century importation, as previously stated. In this paper, the spotted animals have thus far been treated as roans; they have never been popular with breeders, consequently, there are relatively few of them—the few (three) Sittyton matings being typical. It is observed from the table that when a mixed color animal is mated, the mixed color offspring tend to be like the mixed color parent—*i. e.*, either largely roan or largely spotted, as the case may be.

TABLE VI

(Calculated from Table I)

Red by spotted gives	23.3 per cent. spotted and	12.7 per cent. roan.
Red by roan gives	4.4 per cent. spotted and	46.6 per cent. roan.
Roan by spotted gives	25.5 per cent. spotted and	45.3 per cent. roan.

The persistence of spottedness in the offspring of spotted parents is accounted for by the fact that the color areas are definite in location and contour and, being independently transmitted, the registering of fortuitously the red or the white phases of the homologous areas of the two spotted parents will generally produce spottedness in offspring. A similar registering of roan and spotted coats would make the spottedness less pronounced.

There are all degrees of the roan condition, varying from

nearly white to nearly red; this may mean that the set of dominant white hairs and the set of recessive white hairs are not each governed by a single determiner, but by a group of either many or few similarly behaving and generally, but not essentially, synchronously moving determiners. This is consistent with the observed fact that all matings into which roans enter produce more roans than any other color. Thus it appears that, as with spotted-

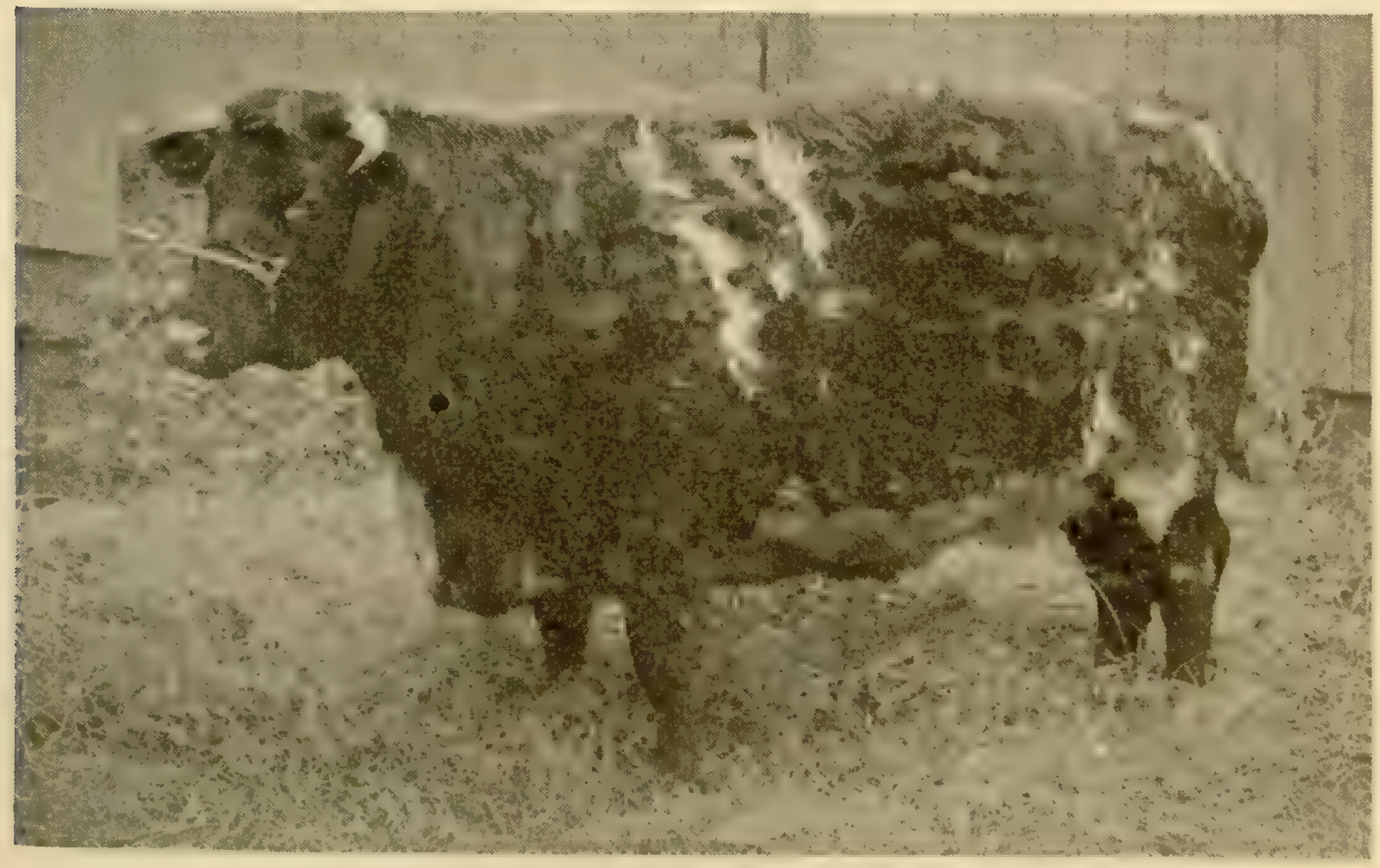


FIG. 6. ROAN LILY.

ROAN LILY 59531. *Roan.*

Courtesy of F. W. Harding, Waukesha, Wis.

Dam—May Lily 59528. *Red.*
Dam's Dam—Mourey May 59529. *Red.*
Dam's Sire—King of Banff (Imp.) 306221. *Roan.*

Sire—Gloster's Choice 284895. *Roan.*
Sire's Dam—Gloster Girl. *Red.*
Sire's Sire—Choice of the Ring 187237. *Roan.*

ness, the degree of roanness is the somatic effect of the fortuitous registering—generally in accordance with the theory of the pure gamete—of the many units composing each of the two independently behaving sets of hairs; this, together with the occasional intra-zygotic inhibition and reaction in response to set conditions, quite completely explains the observed facts. Thus the registering of pigments and patterns may give a measurable somatic

effect in inheritance without a specific chemical unit determiner for such effect, and the spotted and roan Shorthorns are not blends in the old sense of the term.

Angus cattle which are black sometimes throw dark red colors, exemplifying the fact that in cattle, as with animal pigments generally, the darker pigments are epistatically dominant over the lighter, hence the cattle colors—black, red, yellow with its variations—are dominant over "albinic" white (w), like the white of the Silkie Fowl, but "positive" white (W), like the white of the Leghorn Fowl and such as that of the British Park cattle, is dominant over any and all pigments. Corroborative of this, recall the instance reported by Prof. Wentworth, wherein pure-bred Holstein cows were bred to a deep red Shorthorn bull, and in the offspring "the color pattern showed no trace whatever of the Shorthorn parentage." Now conceive the white Shorthorn coat to be made up of an admixture of "albinic" and "positive" whites, and let the duplex red be mated with the white of this nature—the offspring are the familiar roans, for the "positive" white persists and the "albinic" white is covered by the red pigment. In explanation of the black cattle crosses: Mate a white Shorthorn of type No. 9, or a roan of type 7 or 8, with a black Angus or Galloway; the dominant white persists, the black covers the red (as in human hair) and the familiar blue-roan hybrid results in exact accordance with the theory of gametic purity. Conceive of the white-faced Hereford mated with the black Angus—the "positive" white persists, the black pigment covers the red and the familiar white-faced, black-bodied hybrid results. Thus it is determined that the white of the areas of the face, the two flank belts and the underline are largely "dominant white," while those of the neck, barrel and quarters are mostly "albinic white."

The old single-unit coat hypothesis, even when amended to permit the simplex condition in some reds and in some whites, does not explain *how* the simplex condition could run the *entire* color gamut; neither has the "first generation blend, later generation segregation" theory yet been

reconciled with gametic purity. The old hypothesis is, therefore, abandoned. The facts demand the companion-trait or unit-complex hypothesis modified to permit of occasional intra-zygotic reactions in response to a definite set of conditions, instead of the single-unit notion, and the 45 case matings instead of the typical 6.

The following table is compiled from data reported in *Biometrika,* 1905, 1906,[3] by Amy Barrington and Karl Pearson from Coates's Shorthorn Herd Book.

TABLE VII

Mating	Offspring						
	Red	Red little White	Roan	Spotted	Total Mixed	White	Total
1. Red by red.....	156	23	6	11	40	0	196
2. Red by roan.....	243	46	324	39	409	4	656
3. Red by white.....	1	2	85	2	89	0	90
4. Roan by roan.....	104	43	286	69	398	84	586
5. Roan by white.....	1	1	47	1	49	24	74
6. White by white.....	0	0	0	0	0	3	3

In addition to this, special search[4] for white-by-white matings yielded 91 cases, giving 1 red, 4 roan and 86 white offspring; in two cases, red-by-red matings were reported to have given white offspring.

The color distribution of this table practically parallels that found in the Cruikshank herd as reported by Mr. Bruce and that of the other compilations herein recorded.

Barrington and Pearson then proceeded with the following criticism:

> . . . No simple Mendelian formula applies rigidly. We find ourselves neglecting sensible percentages of occurrences incompatible with the theory of the pure gamete.[5]

It is true that the first studies in color in Shorthorn cattle suggested the single-unit color coat hypothesis and as late as 1909 James Wilson, of the Royal College of Dublin, in his interesting book on the "Evolution of British Cattle," suggested this hypothesis. It is not, however, the sole possible Mendelian interpretation, but rather the

[3] *Ibid.,* pp. 427–464.
[4] *Ibid.,* p. 441.
[5] *Ibid.,* p. 454.

preliminary working analysis. The "sensible percentages" that Pearson objects to also impel the most ardent adherent of the pure gamete theory to discard the single-unit color coat hypothesis and to seek the unit—however great or small—that does behave in the expected fashion. We must agree with the above criticism that the incompatible percentages and the exceptions are too persistent to ignore; such percentages simply indicate that the

FIG. 7. RED LADY 6TH.

RED LADY 6TH 86626. *Red.*

Courtesy of F. W. Harding, Waukesha, Wis.

Dam—Red Lady (Imp.). *Red, little White.*
Dam's Dam—Roan Mary. *Roan.*
Dam's Sire—Cornelius 226511. *Red.*

Sire—Baron Sultan 300788. *Red and White.*
Sire's Dam—Athene of Riverdale. *Red.*
Sire's Sire—Whitehall Sultan 163573. *White.*

ultimate unit, or unit-behaving group of characters, is not isolated, and that besides gametic segregation there is occasionally intra-zygotic reaction. The old hypothesis then must be abandoned and another better fitting the facts must be worked out. Among other things the behavior of the unit complex must be studied. Thus, if a Shorthorn is crossed with an Angus, the pure gamete theory does not lead us to expect a series of "blends" or of one of the pure parental types in the F_1 generation and

25 per cent. pure Shorthorn, 50 per cent. blends and 25 per cent. pure Angus in the F_2 generation. If all the independent units moved with absolute synchronism this would be expected, but they are genetically independent and the laws of chance demand that the greater the number of units the more intricate becomes the task of extracting an animal with the combination of a great number of arbitrarily selected traits such as compose any of the pure breeds of domestic animals.

Barrington and Pearson in referring to the blue-gray hybrid and white Shorthorn cross give evidence showing that sometimes blue-gray, sometimes "grizzled" and sometimes white animals result.[6] Quoting Mr. Hodgson, they say: "This cross gives white cattle which are not, however, to be reckoned as pure white Shorthorns."[7] If all the characters essential to differentiating "pure-bred" Galloway and "pure bred" Shorthorn cattle from each other were reduced to their ultimate inheritable units, the laws of chance having free play, we should expect in F_2 one "pure-bred" Shorthorn and one "pure-bred" Angus in 4^n individuals—in which n is the number of ultimate units. A conservative estimate would certainly make this number at least a score, but more likely a hundred or a thousand. Taking into consideration the fact that the phases of the units patent in Shorthorn and Angus cattle are not uniformly dominant or recessive, that the same units that distinguish Shorthorns from cattle in general may not also distinguish Angus from cattle in general, it is obvious that the chance of producing a "pure" animal in F_2 from such a combination is very remote. Thus, if the differentiating traits be uniformly dominant or recessive and only ten in number, the chance of securing such a combination would be one in 1,048,576. The close and exceptional fitting of many cases to the simply four-part Mendelian ratio is the only conclusive evidence of the location of the ultimate unit. It is infinitely easier to approximate one of the

[6] *Ibid.*, p. 433.
[7] *Ibid.*, p. 433.

parental types by breeding back to the desired type—the "pure sire" method— than to extract it from F_2 hybrids by the operation of the laws of chance. In the general run of cattle the 7/8 grades are quite like the pure types; 15/16 grades are much more so, while 31/32 or 63/64 are generally so like the pure breed as to be, except for arbitrary rules, eligible for registration. All of which tends to support the pure gamete theory, in that under such a process the laws of chance rapidly "quarter out" the foreign units, albeit rigid selection can, of course, as it often does, maintain any one of the mongrel types indefinitely. If the number be great, the longer the process and the more likelihood of "reversion." The theory of the pure gamete is not inconsistent with the somatic blend in F_1; in fact, it demands it in the coarser aspects. Such a blend indicates that a unit complex rather than a single unit is under observation.

All the data so admirably collected by Barrington and Pearson yield most readily to a Mendelian interpretation, if by such interpretation is meant the purity, segregation and fortuitous recombination of the unaltered determiners of unit characters, provided such interpretation is not held to be inconsistent with frequent intra-zygotic reactions between the determiner and some antibody occasioned by the definite relative concentration and intimacy of the two bodies. They reject a Mendelian interpretation on the grounds that the whole coat does not behave as a single unit. Gametic purity of the unit character might as well be rejected on the grounds that the whole animal with its thousands of characters does not so behave, or that there are occasional intra-zygotic reactions causing mutations. In mentioning the types of cattle going into the making of the Shorthorn, they continue:

> Upon the ingredients just referred to, the breeders had to work when pedigree cattle breeding, which is scarcely more than a century old, came into vogue. The Shorthorn had possibly arisen from four races: the Celtic, a Romano-British, an Anglo-Saxon and the "Dutch" and even some of these are mixtures. . . . Thus the Shorthorn Red may

have had three sources—an Anglo-Saxon red, the red of the Dutch flecking, and the supposed Celtic red. The white may have come through the Romano-British, through the Anglo-Saxon white or possibly through the white in the Dutch. The particolors and the roans are of equally doubtful origin, although it probably is safe to assert that they are due to the breeds of latest importation; and it thus seems fairly impossible to determine *a priori* how many distinct red, roan, particolor or white types may really exist in the case of the Shorthorn. The importance of this statement for any Mendelian interpretation must be obvious. We may have reds which are dominant, recessive or even heterozygous to white or even to other reds, and the search for a Mendelian formula becomes very elusive. . . . We have seen that there is historically a possibility of two strains of red and two strains of white having been mingled in the Shorthorn. Determinants representing particolor and white markings can undoubtedly be introduced also; we confess to having made an attempt from this standpoint which shattered with further examination of Table I.—but the introduction needs a wider practise than we can boast of in inventing Mendelian formulæ and until we are more convinced than we are at present of the soundness of such formulæ we should prefer to leave the invention to those who have had it. Coates Herd Book presents a wide range of material and whatever we may think of the categories selected, the record has been made by persons in absolute ignorance of recent controversies about heredity. It is therefore really impartial material for Mendelians to unravel. . . . It would thus seem that no simple Mendelian formula can possibly fit the Shorthorn cases. Roughly, such a formula approaches the data in one or two points but the roughness appears inconsistent with a theory of Mendelism being due to the purity of gametes. It is of course clear that the introduction of a complex allelomorph may improve matters, or the differentiation of whites and reds into different classes, homozygous and heterozygous. Increase in the number of available variables usually does give better fits.[8]

The whole color problem in Shorthorns is a complicated study in mongrelism and no single simple four-part Mendelian ratio can be expected to explain it. Instead of a single unit or a single uniformly dominant or recessive series, there are two genetically independent unit-behaving groups of units—one dominant, the other recessive in their companion, *i. e.*, their white phases. However, such companion traits—if the somatic blend is considered as simplex—when undistinguished, will give the

[8] *Ibid.*, p. 444.

simple four-part Mendelian ratios in 42 case matings out of 45, the exceptions being matings 28, 29 and 36. In summing up the coat-color inheritance of blue-gray cattle, Barrington and Pearson say on page 435, "It will need a complex allelomorph to describe these color changes, if, indeed they can be described at all." With this it must be agreed. The "complex" allelomorph is, however, not so complex, after all; the complex is simply a group of

FIG. 8. AVONDALE.

similar units each independently transmitted. If they were less uniform in their somatic aspects they would not be so confused. The task of segregating the unit becomes more difficult but not at all impossible.

Barrington and Pearson emphasize the statement that the evidence of the breeders of the blue-grays is that a white Shorthorn bull of white parentage is greatly to be preferred to one of roan parentage, inasmuch as the former type invariably gives the desired blue-gray color —referring to Mr. deVere Irving:

AVONDALE 245144. *Roan.*

Courtesy of Carpenter and Ross, Mansfield, Ohio.

Avondale
Roan **245144**
Jan. 5, 1905
E. S. Kelly
Yellow Springs, Ohio

- **White Hall Sultan** ***White*** **163573** — J. Deane Willis
  - **Bapton Sultan** ***Roan*** **163570** — J. D. Willis
    - **Bapton Victor** ***Roan*** **163571** — J. D. Willis
      - **Count Victor** ***Roan*** **132574** — J. D. Willis
      - **Cowslip** ***Red*** **Vol. 41 p. 678 E.** — J. D. Willis
    - **Moon Daisy** ***Red*** **Vol. 42, p. 704 E.** — J. D. Willis
      - **Captain of the Guard** **Red** **132059** — A. Cruickshank
      - **Wiltshire Daisy** ***Red and White*** — J. D. Willis
  - **Imp. Bapton Pearl** ***Roan*** **Vol. 48, p. 368** — J. D. Willis
    - **Count Lavender** ***Roan*** **132575** — W. Duthie
      - **Norseman** ***Red*** **132576** — A. Cruickshank
      - **Sweet Lavender** ***Roan*** **Vol. 33, p. 307 E.** — W. Duthie
    - **Primrose 2d** ***Roan*** **Vol. 39, p. 228 E.** — W. Duthie
      - **Golden Crown** ***Roan*** **157369** — A. Cruickshank
      - **Primrose** ***White*** — A. Davidson
- **Imp. Avalanche 2d** ***Roan*** **Vol. 60, p. 655** — C. H. Jolliffe
  - **Mescombe** ***Red, little White*** **222700** — S. H. Allen
    - **Captain Lavender** ***Red*** **222673** — J. D. Willis
      - **Captain of the Guard** ***Red*** **132059** — A. Cruickshank
      - **Lavender 58th** ***Roan*** — A. Cruickshank
    - **Meadow Pipit 7th** ***Red*** — S. H. Allen
      - **Kinsman 53d** ***Red, little White*** **222691** — R. Wood
      - **Meadow Pipit 4th** ***Red, little White*** — S. H. Allen
  - **Avalanche** ***Roan*** **Vol. 45, p. 786 E.** — W. A. Mitchell
    - **Sittyton Scarlet** ***Red*** **151407** — A. Cruickshank
      - **Cumberland** ***Roan*** **50626** — A. Cruickshank
      - **Amaranth** ***Red*** **Vol. 34, p. 308 E.** — A. Cruickshank
    - **Averne 10th** ***Roan*** — J. Bruce
      - **Snowball** ***White*** **140037** — J. Bruce
      - **Averne 6th** ***Red*** — J. Bruce

He finds on using a white bull of roan parentage that the offspring are liable to come dark, some almost black, in color and others very dark blue-gray.[9]

No better material for Mendelian interpretation than this could be offered. It simply means that the white bull of "white parentage" is more likely to be of type "9" (a roan bull of type 7 or 8 would do as well); the whole becomes a mating of type No. 20, which expects 100 per cent. roans—black taking the place of red the

FIG. 9. AVONDALE'S FIRST CALVES.

roan becomes blue-roan or "blue-gray." A white bull of "roan parentage" is more likely to be of type "6" (a roan of type 4 or 5 would do as well—see matings Nos. 5 and 14), which mated to a pure black would produce 50 per cent. blue-roans and 50 per cent. blacks, in accordance with a mating of type No. 23. Wild white cattle which occasionally drop red or black calves, when crossed with a white Shorthorn produce white offspring. Such a female offspring when bred to a white Shorthorn bull "may produce a considerable percentage of both roan and red as well as of white calves."[10]

[9] *Ibid.*, p. 432.
[10] *Ibid.*, p. 442.

AVONDALE'S FIRST CALVES

Courtesy of Carpenter and Ross, Mansfield, Ohio.

Sire—Avondale. ROAN.
Sire's Dam—Imp. Avalanche 2d. *Roan.*
Sire's Sire—Whitehall Sultan. *White.*
Sire's Dam's Dam—Avalanche. *Roan.*
Sire's Dam's Sire—Mescombe. *Red, little White.*
Sire's Sire's Dam—Imp. Bapton Pearl. *Roan.*
Sire's Sire's Sire—Bapton Sultan. *Roan.*

Calf No. I. Colonel. *Dark Roan.*
Dam—Chrysanthemum. ROAN.
Dam's Dam—Christina. *Roan.*
Dam's Sire—General White. *White.*

Calf No. II. Max Rosewood. *Roan.*
Dam—Rosewood 86. ROAN.
Dam's Dam—Rosewood 81. *Roan.*
Dam's Sire—Pride of Day. *Roan.*

Calf No. III. Wall Street. *White.*
Dam—Wedding Gift 16. ROAN.
Dam's Dam—Wedding Gift 12. *Roan.*
Dam's Sire—Royal Prince. *Roan.*

Calf No. IV. Sir Collin Campbell. *Red, little White.*
Dam—Ury Lassie. RED, LITTLE WHITE.
Dam's Dam—Ury of Greenwood. *Red, little White.*
Dam's Sire—Royal James. *Red.*

Calf No. V. Max Clipper. *Red.*
Dam—Miss Council. ROAN.
Dam's Dam—Christina. *Roan.*
Dam's Sire—Council. *Roan.*

Precisely this phenomenon was paralleled experimentally and given a clear Mendelian explanation by Davenport,[11] who mated the dominant white of the Leghorn fowl with the recessive white of the Silkie. The F_1 generation, save for some red on the wings of the males, was white; this F_1 generation mated *inter se* gave some individuals with the typical ancestral Jungle fowl coloration. The fact that the Park cattle generally breed white but occasionally throw a red or a black calf means that generally the germ cell formula is (W_2R_2), which will throw all white, but sometimes is (W_wR_2), a strain of which introduced into a breed will throw the "occasional red calf." The introduction of a strain of partial albinism seems to effect this cleavage and apparently is brought about as follows:

[11] "New Views about Reversion," *Proceedings of the American Philosophical Society,* Vol. XLIX, No. 196, p. 294.

Wild White Cow			*Offspring*			
Body areas 1 and 2						
Germ cells W_2R_2			1	2		
White Shorthorn Bull No. 6			8 WwR_2	WwRr	*White*	F_1 100 per cent. White.
Body areas 1		2				
Germ cells WwR_2		w_2r_2	8 W_2R_2	WwRr	*White*	
1		2				
$2\ W_2R_2 + 2\ WwR_2$		4 WwRr				

Now mate a female of one of these types—*e. g.*, $1/W_wR_2$ $2/W_wR_r$ with a white Shorthorn bull—*e. g.*, one of type No. 6.

Areas	1	2
Hybrid cow	WwR_2	WwRr
Bull No. 6	WwR_2	w_2r_2
1		2
$W_2R_2 + 2\ WwR_2 + w_2R_2$		WwRr + w_2r_2 + Wwr_2 + w_2Rr

1	2	
W_2R_2	*WwRr*	*White*
W_2R_2	w_2r_2	*White*
W_2R_2	Wwr_2	*White*
W_2R_2	w_2Rr	*Roan*
2 WwR_2	*WwRr*	*White*
2 WwR_2	w_2r_2	*White*
2 WwR_2	Wwr_2	*White*
2 WwR_2	w_2Rr	*Roan*
w_2R_2	*WwRr*	*Roan*
w_2R_2	w_2r_2	*Roan*
w_2R_2	Wwr_2	*Roan*
w_2R_2	w_2Rr	*Red*

No theory not involving the purity—*i. e.*, chemical identity, of the determiner and its segregation and recombination in unaltered form, together with occasional intrazygotic inhibition and reaction in response to specific conditions, can explain the facts reported by Barrington and Pearson, which facts of observation tally with those reported from many other sources.

Confirmatory of the declaration that the white of the wild Park cattle is dominant white, the following evidence by Storer—referring to the Chartley cattle—is offered:

> Whatever cows were put to the white bulls, the calves came almost invariably the color of their sires; the only instance he remembered to the contrary being that on one occasion a dark-colored cow produced a spotted calf. Thus were singularly confirmed at Chartley two of the facts which Bewick relates with regard to Chillingham—the existence of the custom and the prepotency of the white sire.[12]

[12] "The Wild White Cattle of Great Britain," p. 239.

And further, in quoting Mr. John Thornton he says:

> The peculiarity most striking was the color; a clear white body, head and neck, with much hair; but the ears, nose, circle around the eyes, and the hoofs were black, and there were a few black spots on the fetlock above the hoof.[13] Black calves are not at all uncommon. . . . When the variation of color occurs the calves are always pure black, "with not a white hair on them" never particolored. . . .[14]

Professor S. Cossar Ewart, of Edinburgh, writes (April 11, 1911):

> Some years ago I saw at Chillingham crosses between these white Park cattle and white Shorthorns—all the crosses were white or light cream color.

Recently under his direction wild Chartley bulls were crossed with domestic heifers. The matings and offspring are indicated by chart No. 2, which was drawn from data supplied by him.

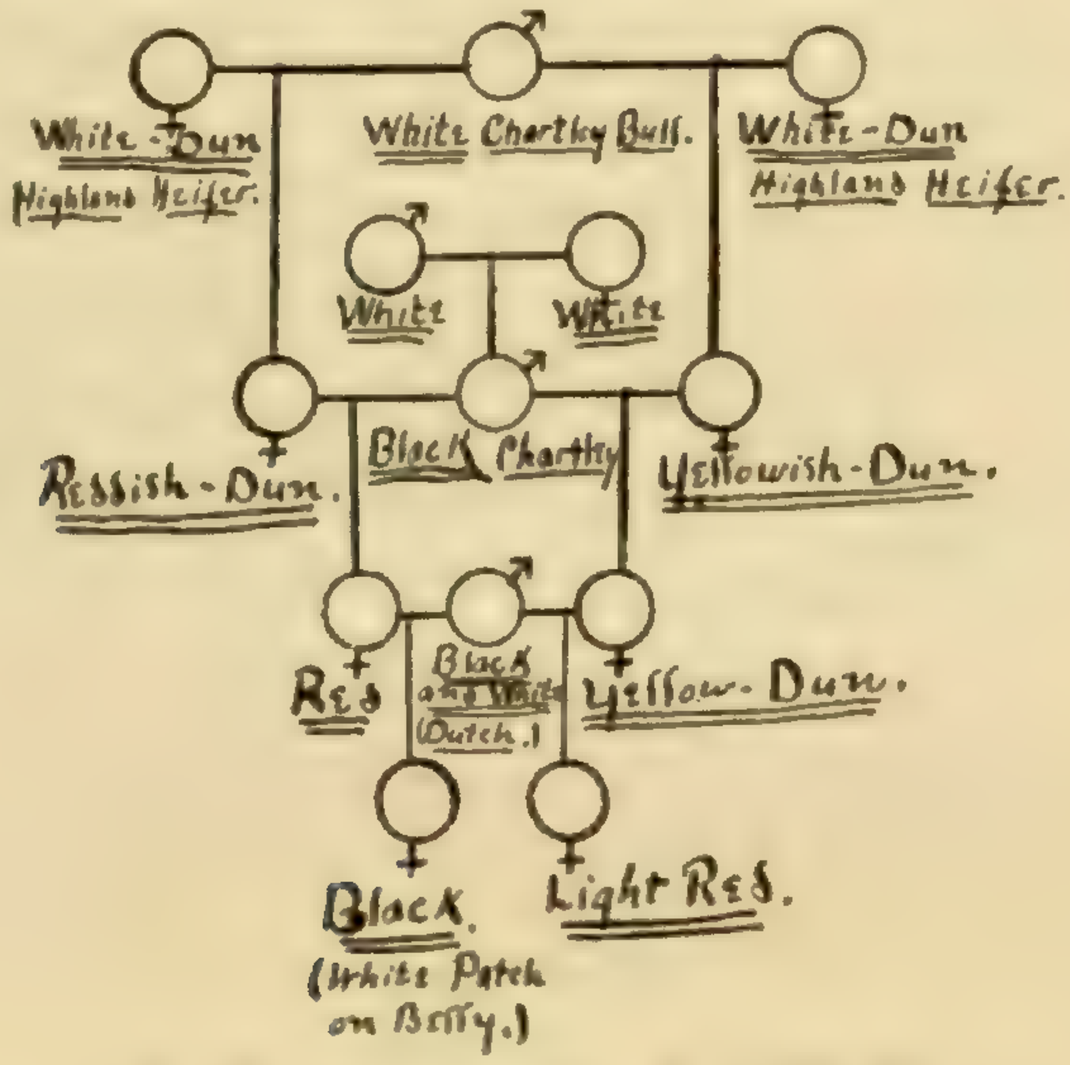


CHART II. Ewart's Experiment.

From this, as from other pedigrees, it appears that the white of the Park cattle is dominant white, that, barring dominant white, the darker pigments are epistatically dominant over the lighter ones, but that neither dominancy and segregation nor the coexistence of several pigments, nor midway blends—all of which may operate here—entirely explains the facts; there must also be occasional intra-zygotic reaction and mutations.

[13] *Ibid.*, p. 241.
[14] *Ibid.*, p. 237.

The behavior of the crest when a crested fowl is mated with a non-crested variety is typical of the behavior of somatic blends tending to obscure gametic segregation. Davenport[15] has shown that there are two genetically independent factors united in the crest: One, erectness of feather growth over a certain area is *dominant* over the normal condition; the other a continued growth of feathers of this area is *recessive* to the normal growth. Hence, in the F_1 generation there is an apparent "blend." the feathers being short but erect. From F_1, however, in subsequent generations, Davenport has extracted a beautiful complete crest. There are many other striking somatic blends—among them the case of the Andalusian fowl, of the human mulatto, and of the human hermaphrodite. Blends are essentially the somatic aspects of the fortuitous combinations of the patent and latent phases of two or more genetically independent units. In this sense Galton's law may justly stand for the general measure of ancestral influence—a measure of the operation of the laws of chance. The existence of somatic blends can not be denied, for they are among the most definite things commonly observed in inheritance. The more cursory the examination and the more general the view of such cases, the more seeming the blend; however, a more minute inspection often reveals the segregation of the parental factors, all of which points towards the minuteness of the unit character and the purity of the gamete. Were blending, in the commonly understood sense a fact, all individuals of a race or a strain would in a few generations become identical with each other. It is the creation of new units by intra-zygotic reactions and intra-gametic intrusions, together with the segregation and recombination of the unaltered ultimate units of inheritance that have given selection such an opportunity for developing so many strains and species.

[15] "Inheritance in Poultry," p. 69.

(*To be concluded*)

STUDIES ON MELANIN—IV

The Origin of the Pigment and the Color Pattern in the Elytra of the Colorado Potato Beetle (*Leptinotarsa decemlineata* Say[1])

DR. ROSS AIKEN GORTNER

Introduction

Among the more important problems in the study of animal pigmentation is the question as to the origin of the color pattern. Perhaps one of the most common of the insects which has a definite color pattern is the Colorado potato beetle (*Leptinotarsa decemlineata* Say), and I have, therefore, investigated the origin of the color in the elytra of this beetle, and have found a possible explanation for the cause of the color pattern.

I have already shown that in all probability the formation of animal pigments is due to the interaction of some chromogen and an oxidase of the tyrosinase type (Gortner, 1910, 1911). I have found evidence which leads me to believe that the same reaction produces the pigment in the potato beetle, and that the color pattern of the elytra is produced by the localized secretion of chromogen.

Historical

In so far as I am aware the only work which has been done on the nature of colors in *Leptinotarsa* has been reported by Tower. In an article on "Colors and Color Patterns in Coleoptera" (1903), Tower discusses the origin of the pigment in the Colorado potato beetle, and repeats his findings in a larger work, "An Investigation of Evolution in Chrysomelid Beetles of the Genus *Leptinotarsa*" (1906). The biological features of the latter

[1] From the Biochemical Laboratory of the Station for Experimental Evolution. The Carnegie Institution of Washington.

work have been reviewed elsewhere (Cockerell, 1907), but, in so far as I can find, the chemical data and theorizings have been passed over. It is evident from a very casual glance at the chemistry, that Tower has strayed from familiar paths and is wandering far afield. I can refer to only a few of his errors here, but these are so obvious as to show that no reliance can be placed upon the chemical findings, much less upon his chemical theorizings.

Perhaps the worst error, inasmuch as Tower bases all of his results as to the nature of the pigment upon this point, is to state (1906, p. 136), "Bottler, working upon the hair of animals and upon silk, has shown these pigments to be azo compounds, and in insects they belong to the same series." The reference which Tower quotes is a book by Bottler (1902) entitled "*Die animalischen Faserstoffe. Ein Hifls- und Handbuch für die Praxis, umfassend Vorkommen, Gewinnung, Eigenschaften und technische Verwendung sowie Bleichen und Färben thierischer Faserstoffe. Nach dem gegenwärtigen Standpunkte der wissenschaft bearbeitet.*" From the title I did not expect to find much original work on the subject of *animal pigments*, neither could I find in any of the biochemical literature any reference which could be so construed as to intimate that animal fibers, especially silk, occurred naturally dyed with azo dyes. I find in Bottler's book references to azo compounds in the chapter on "Das Färben animalischer Faserstoffe" *and in each instance the references are to azo dyes with which to dye the animal fibers. In almost every instance Bottler gives the origin of the dye employed, as "M. L. Br." (Meister, Lucius and Brüning) or "Fr. Bay." (Fr. Bayer & Co., in Elberfeld) together with explicit directions as to the composition of the dyeing bath.* Bottler does mention the naturally occurring pigments by stating on page 36 that "dark-colored wools are usually used in their natural color or dyed dark, as it is only with great

difficulty that they can be bleached'': and on page 44 ''one uses camel hair in the natural color or dyed dark inasmuch as it can not be bleached.'' This is the only connection in which the natural-occurring pigments are mentioned.

Tower states (1903, p. 63) that:

> The chemical nature of colors is a problem most difficult of investigation, chiefly because such energetic measures are necessary to get the color into solution that there is every reason to suspect that it is no longer the same as that in the cuticula. With solutions of *P. cornutus* in HCl or H_2SO_4, various tests were made, which established the fact that it is much like some of the benzine derivatives, and the spectra of this solution and of permanent brown are identical and closely similar to that of Bismarck brown. There is, however, a great difference between the solution of cuticula color and Bismarck brown, the former being a *colored substance* and the latter a *coloring substance.*
>
> Cuticula colors in acid solution are decolorized by reducing agents such as tin and HCl or strong alkalis. If, however, the decolorized solution is treated with a mild oxidizing agent, part or perhaps all of the color is restored. In the process of decolorization the solution passes from deep brown to lighter shades, to yellow, and eventually to a colorless solution. According to Stecher and others, fast brown is a diazo compound belonging to the group of amidoazo and oxyazo compounds, which form colored solids varying from yellow to deep brown. These diazo, oxyazo, and amidoazo compounds are soluble in alcohol, as is this cuticula color,[2] and when in solution are rendered colorless by reducing agents, thus forming colorless azo, or hydrazo compounds, which, by mild oxidation, may be reconverted into yellow- or brown-colored diazo, oxyazo, or amidoazo compounds. There is thus a very close agreement between the reaction of cuticula color and the diazo, oxyazo, and amidoazo compounds to reducing and oxidizing agents. In these and in other characters the cuticula colors resemble these benzine derivatives, but not in any respect do they resemble other colored substances or dyes known to organic chemistry. The existence of azo compounds has been recognized by Bottler in the hairs of animals and in silk fibers, where they function as pigments and have some of the structural peculiarities of cuticula color. I feel perfectly certain, therefore, that these cuticula colors are azo compounds, a conclusion based upon the following characters: (1) their colors; (2) solubility;

[2] On page 41 of the same work Tower states that these cuticula colors are ''insoluble in water, alcohol, ether, oils, weak acids or alkalis. Soluble in strong concentrated mineral acids with dissolution of the cuticula.''

(3) behavior to oxidizing and reducing agents; (4) crystallization; (5) spectrum; and (6) their decomposition products.

Let us see what of real value these characters possess:

1. If color is any criterion, all colored objects must contain azo dyes, inasmuch as azo compounds occur in almost every possible shade of color,

2. If the data which Tower gives on page 11 (1903) be referred to we find

Cuticula colors	Black, Dark brown, Brown, Straw yellow	Located in primary cuticula	Permanent. Insoluble in water, alcohol, ether, oils, weak acids or alkalis. Soluble in strong concentrated mineral acids with dissolution of the cuticula.

These are not the characteristics of the azo compounds, for azo compounds are soluble in alcohol and in many cases are very soluble in water. The "amidoazo" compounds are soluble in weak acids and the oxyazo compounds are very soluble in weak alkalis. *The characters which Tower gives are, however, exactly those characters which are possessed by the melanins.*

3. Tower has made a great mistake when he states that azo compounds are reduced to colorless bodies and then reoxidized to colored diazo, oxyazo or amidoazo compounds by mild oxidizing agents. *When azo compounds are reduced by tin and hydrochloric acid the azo union is broken, each nitrogen atom yielding an amino group, and the colored compound can not be regenerated by mild oxidation, but the original diazotization and coupling must be repeated before a color results.* For example we reduce Congo red and we get benzidine and "naphthionic acid" neither of which gives a color on mild oxidation. (See Mulliken (1910), p. 26, footnote.)

$$\begin{matrix} C_6H_4\text{—}N{=}N\text{—}C_{10}H_5(SO_3H)(NH_2) \\ | \\ C_6H_4\text{—}N{=}N\text{—}C_{10}H_5(SO_3H)(NH_2) \end{matrix} + 2H_2$$

$$= \begin{matrix} C_6H_4\text{—}NH_2 \\ | \\ C_6H_4\text{—}NH_2 \end{matrix} + 2C_{10}H_5(SO_3H)(NH_2)_2.$$

There are, to be sure, dye stuffs (for example, indigo), which do reduce to colorless compounds, or leuco bases,

and which reoxidize to the original color and compound, *but the azo compounds are distinguished from these colors by the fact that no reoxidation takes place.*

4. I have been unable to find any data as to the crystal form of cuticula pigments. All writers report that they are non-crystalline. If Tower succeeded in preparing crystals he has succeeded where every one else has failed. The azo compounds, on the other hand, are usually easily obtained in crystal form.

5. As to the value of the spectrum I will quote Tower's own words (1903, p. 56).

> The study of animal and plant pigments has been carried on almost entirely by means of spectrum analysis. . . . There is, however, very grave doubt as to the value of such spectrum work. After spending several months in the analysis of cuticula pigment of Coleoptera, Lepidopterous larvæ, and Hymenoptera, I discarded as worthless all of my results, because in no case was I able to obtain a spectrum of sufficient permanence, or one that had absorption bands of enough constancy, to be reliable. The same solution with the same apparatus and light will vary in its spectrum from day to day. Moreover, any slight change in acidity or alkalinity, or in dilution or concentration, etc., will produce a variation in the spectrum.

6. In regard to the decomposition products of cuticula pigments, I can find no data in Tower's paper, so that I do not know in what respect they may resemble known organic compounds. Enough has been shown, however, to prove that Tower's statement (1906, p. 136), "we are safe, then, in concluding that these cuticula pigments are azo compounds, but whether they are azo, diazo, oxyazo, or amidoazo[3] is not known," is entirely without foundation.

[3] For those who are not familiar with this nomenclature I will give here an example of the formula of each class:

Azobenzene, $C_6H_5—N{=}N—C_6H_5$,
Diazobenzene, $C_6H_5—N{=}N—OH$.

Tower probably refers to *Disazo* compounds, inasmuch as diazo compounds are very unstable and are not coloring matters.

Disazobenzene, $C_6H_5—N{=}N—C_6H_4—N{=}N—C_6H_5$,
Oxyazobenzene, $C_6H_5—N{=}N—C_6H_4OH$,
Aminoazobenzene, $C_6H_5—N{=}N—C_6H_4NH_2$.

Other examples of this chemistry are numerous, but I can only mention one or two. Tower states (1903, p. 54) "Sundwick and Ledderhose conclude that chitin is an amido derivative of *a carbohydrate having the formula* $C_6H_{100}O_{50}$."[4] I was willing to allow this as an error in proof-reading had not the same $C_6H_{100}O_{50}$ occurred again on page 55, where he adds "*and hence glucoside, like cellulose,*[5] and other plant substances."

Again I quote from the 1906 paper (p. 123) "Griffiths farther isolates and studies a green pigment which is allied to uric acid or is a uric acid derivative called lepidopteric acid ($C_{11}H_{10}Az_2N_8O_{10}$?)." I have not seen Griffiths's paper (1892), but, from the formula which Tower gives, I would say that the question mark is well placed, inasmuch as the English form of nitrogen is not known to differ from the French variety. Some of the other errors will be referred to in connection with my work.

EXPERIMENTAL

The Formation of the Pigment by Oxidation.—The material employed was the pupæ and adults of the Colorado potato beetle, *Leptinotarsa decemlineata* Say. Large larvæ were secured in the field and placed in battery jars, provided with abundance of fresh potato stalks, and containing about four inches of sifted soil in the bottom. The top of the jar was covered with mosquito netting. Within a few days all of the larvæ had entered the soil and had pupated. When the adult beetles emerge from the pupal skin, the elytra are an almost uniform light yellow color, and upon this surface the lines of the darker color pattern shortly appear. In accordance with my former work I have found that this pigmentation is an oxidation, induced by an oxidase of the tyrosinase type.

Tower (1903, p. 58) states that he tested the rate of pigmentation when the pupæ were kept in an atmosphere

[4] My italics.

[5] My italics. Cellulose is in no way related to the glucosides.

containing respectively "O_2 40 parts, N_2 80 parts; O_2 60 parts, N_2 80 parts; O_2 80 parts, N_2 80 parts, and O_2 pure. In the first two no changes were noted, but in the third there was a large mortality, showing that the amount of O_2 had become toxic and the pigmented areas were small and weak. The same results were attained in a more marked manner with pure O_2."

Tower's results in this instance are easily accounted for, inasmuch as a very small quantity of oxygen is consumed in the process of pigmentation and even in normal air the oxygen is present in enormous excess. The rate of pigmentation is, in all probability, at a maximum even when the oxygen is present in very small concentration. Tower further adds (1903, p. 58): "A second set of experiments consisted in diminishing the O_2 present, but even although O_2 was absent, pigmentation was not changed. A third set consisted in placing pupæ in an atmosphere of CO_2, N, H, and pigmentation, if about to begin or already begun before the pupæ were placed in the gas, was not retarded or changed." Tower does not state what precautions were used to ensure the entire absence of oxygen. *I have found that when all oxygen is absent, no pigmentation takes place.*

Newly emerged adults, whose elytra showed no trace of brown pigment, were placed in gas wash bottles which were provided with a tubulated ground glass stopper, arranged in such a manner that when the stopper is turned slightly the stream of gas is cut off and the bottle is tightly closed (see Eimer and Amend's 1910 Catalogue no. 3658). A current of washed carbon dioxide, from a Kipp apparatus, was then passed through the bottle for twenty-four hours and then the gas was shut off by turning the stopper slightly. *In every instance the elytra of the beetles remained colorless as long as they remained in the carbon dioxide* and if removed to the air, or else if the carbon dioxide were displaced by a stream of pure oxygen, before decomposition set in, pigmentation pro-

ceeded at once. Other beetles were kept in the air as a check upon the results, and in some instances one elytron was removed, and either the beetle minus one elytron was placed in the carbon dioxide and the other elytron kept in the air as a check, or *vice versa*. The same results were obtained when pure hydrogen was used instead of carbon dioxide. I found that it was impossible to obtain entire absence of oxygen when either rubber or cork stoppers were employed, for on long standing some traces of oxygen, apparently, diffuse through the rubber or cork, and cause pigmentation to proceed.

If a beetle with unpigmented elytra be kept submerged in water by means of a small weight, for example in a test tube under a ten cent piece, no coloration appears in thirty-six hours, while in a check the pigmentation was complete in twelve hours. When, however, the beetles were removed from the water and exposed to the air, pigmentation proceeded at once. In most cases the beetles revived after having been submerged for thirty-six hours, as did those that had been forty-eight hours in carbon dioxide. Heating an unpigmented elytron at 70° for one minute totally inhibits pigment formation. The above results are identical in every respect with those which I have reported in the case of the periodical cicada (1911) and the meal worm (1910 b.), so that there can be no doubt that the formation of the pigment in the elytra of the Colorado potato beetle is an oxidation. Tower states (1903, p. 53) that the cockroach, *Phyllodromia germanica* Linn. was used in contributing to his conclusions, and Phisilax (1905) has since shown that in this material the pigmentation is due to an oxidation induced by a tyrosinase.

Evidences of Enzyme Action.—Tower claims to have shown the presence of enzymes by finding *stained zymogen granules* in some of his sectional material. He states (1903, p. 60), "it was impossible to prove the existence of a zymogen in the hypodermis of much of my

material, as almost all of the best of it was in sublimate-acetic-acid fixation, which does not fix zymogens well, but dissolves them and leaves vacuoles where the granules should have been. . . . With Berenyi and picric acid mixtures some zymogen granules were preserved, but the rest of the material was so bad that the preparations were useless. The account of the zymogens and their part in pigmentation is based on material from *L. decemlineata* and *C. femorata*. For demonstrating the presence of substances, probably zymogens, I used iron hæmatoxylin, which is fairly good, and Bensley's stain for zymogens.''

I do not know by what right one can designate a stained granule as a zymogen when we do not know whether zymogens exist as distinct bodies or not. Zymogen is only a term which we use to state the fact that in some cases there is, apparently, the sudden appearance of enzyme action where no enzyme action could be previously detected. We call the mother substance of this enzyme a zymogen, but since the term ''enzyme'' is only another term for a peculiar kind of energy, which may some day be shown to be only a catalysis, or other physical phenomenon, we have, at present, no basis for believing that either enzymes or zymogens can be stained by definite stains.

Tower states that he has prepared an enzyme which is responsible for the production of pigment. and which causes the hardening of the primary cuticula. To this ''enzyme'' he has given the name ''chitase.'' The method of preparing this enzyme is given on page 60 (1903), and on page 138 (1906). Pupæ were ground with quartz sand and the mixture extracted with 35 per cent. alcohol containing 2 per cent. of acetic acid, or with 50 per cent. alcohol containing 10 per cent. of glycerol. ''Dilute alcohol and acetic acid served the best, as it gave the largest precipitate upon the addition of 95 per cent. alcohol. The white, rather flocculent, precipitate pro-

duced was separated by filtration, redissolved in alcohol and acetic acid, and reprecipitated several times, and finally used in 30 per cent. alcohol containing one tenth per cent. acetic acid.'' Into this solution were suspended pieces of primary cuticula, taken before pigmentation had begun to develop. ''The result was that in about thirty-six hours the cuticula had become brown, being first drab, then pale brown, then full brown. Beyond this, coloration did not advance. It was uniform over the entire surface, but, although areas where spots normally develop were present, no tendency to spot formation was observed.''

This does not prove that the solution which Tower prepared contained enzymes, for the pieces of unpigmented cuticula which were used as the testing material may have contained sufficient enzymes to produce the pigmentation. Tower does not mention that he used a check of distilled water in place of the ''enzyme'' solution. I have repeated this part of the work, and for the piece of the primary cuticula I have used the fresh elytron, taken before the pigmentation had begun to develop. I find that there is an appreciable difference in the rate of the development of the pigment when the elytron is placed in the ''enzyme'' solution or in distilled water, *and that this difference is in favor of the distilled water*. The color is distributed more over the entire surface in the case of the enzyme solution, but I find that this is probably due to the fact that the precipitate contained some of the chromogen and when this came in contact with the tyrosinase on the surface of the elytron, pigment was produced. *Tower's ''enzyme'' solution, if it does contain an enzyme, does not contain the enzyme which causes the pigmentation, for it gives none of the tests for oxidases.* Oxidases are destroyed by solutions that are slightly acid so that this is probably one of the reasons why his preparations did not give more positive results. Another reason could be found

in the high percentage of alcohol which was used both to extract the enzyme, and as a solvent.

The Isolation of a Tyrosinase.—Phisalix (1905), Dewitz (1902), Roques (1909) and Durham (1904), as well as myself (1910 b.) (1911), have shown that the production of melanin is caused by the action of an oxidizing enzyme of the tyrosinase type upon some oxidizable chromogen, which may, in some instances, be tyrosin. My first step was, therefore, to ascertain whether or not tyrosinase were present in the potato beetle. I found that it was present in large amounts in the beetles that were collected in the field. In order to make sure that there was no mistake, I tested some of the potato leaves, and there I found abundance of tyrosinase. I found, however, that if I removed large larvæ to the laboratory and kept them without food until they pupated, that the body contents of these three or four days old pupæ gave no test for the enzyme. As a final precaution, however, I used only the unpigmented elytra of beetles which had transformed from such pupæ. In this manner there seems to be no possibility that the food could have contaminated the material, for a period of a least twelve days without food must have elapsed between the securing of the larvæ and the removing of the unpigmented elytra from the adult beetles. The elytra, which showed only a faint trace of the color pattern which was to develop, were ground with quartz sand in an agate mortar, and the mixture leached with distilled water containing a few drops of chloroform. The filtered solution was clear, gave an intense blue with a drop of tincture of gum guaiac, produced a rapid darkening in solutions of tyrosin, leading to the deposition of the typical black precipitate, lost its activity at 70°, or in the presence of *meta* di phenols [see Gortner (1911 b.)], and behaved in every way identically like other preparations of tyrosinase which I have reported from other sources. *There can be no doubt that if the pigmentation in other instances is*

caused by the action of a tyrosinase, the same cause produces the color pattern in Leptinotarsa.

The Cause of the Color Pattern on the Elytra.—If the pigmentation is due to the oxidation of a chromogen by an enzyme, the color pattern may develop in four ways. (1) The enzyme may be present over the entire body and the chromogen may be localized. (2) The enzyme may be localized and the chromogen secreted over the entire body. (3) Both enzyme and chromogen may be localized in those spots which form the color pattern. (4) Those spots which lack color may be pigmentless because there is an inhibitor to pigment production present. I have found that in all probability the first hypothesis is the true one, for, although the pigmentation is not much more general when an unpigmented elytron is placed in a solution of tyrosinase, when such an elytron is floated upon a solution of tyrosin the entire elytron becomes pigmented. Apparently, therefore, the chromogen is localized and the enzyme is secreted over the entire surface.

SUMMARY

It has been shown that Tower's statements as to the nature of the cuticula pigments, and the methods of pigment formation, are based upon wrong interpretations of his results, and upon errors in the application of chemical data. The cuticula pigment is not an azo compound but belongs to the melanins.

The pigmentation of the elytron of the Colorado potato beetle (*Leptinotarsa decemlineata* Say) is produced by the interaction of an oxidizing enzyme of the tyrosinase type, and an oxidizable chromogen. The color pattern is caused by the localized secretion of chromogen.

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SHORTER ARTICLES AND DISCUSSION

A NOTE ON CERTAIN BIOMETRICAL COMPUTATIONS[1]

1. It is a well known fact that curves of individual growth, in which some size character of the organism is taken as ordinate, and time as abscissa, are closely related to a logarithmic curve. To Pearson[2] belongs the credit of first demonstrating this concretely by fitting a logarithmic curve to growth data. Since that time a number of other students[3] of growth have made use of such curves in graduating observational data.

Now while the simplest logarithmic curve

$$y = a + b \log x \qquad \text{(i)}$$

is probably only very exceptionally (if ever) followed precisely in the growth of an organism, yet it certainly represents the general type towards which many observational growth curves tend. In the practical analysis of growth data it is often found to be extremely helpful as the first step to fit such a curve as (i) or a simple variant of it in which a "line" term is added, as in

$$y = a + bx + c \log x. \qquad \text{(ii)}$$

Actually finding out by trial just wherein a curve like (ii) fails to fit the data—if it does fail—will usually give one the clue as to the way in which the curve must be modified in order to graduate the observations satisfactorily.

In fitting a curve like (ii) to a series of observations by the method of least squares the type equations are as follows:

$$\left.\begin{aligned} &S(y) - na - bS(x) - cS(\log x) = 0, \\ &S(xy) - aS(x) - bS(x^2) - cS(x \log x) = 0, \\ &S(y \log x) - aS(\log x) - bS(x \log x) - cS(\log x)^2 = 0, \end{aligned}\right\} \qquad \text{(iii)}$$

where S denotes summation for the n values of the variables.

Now it is evident that, of the 11 summations included in these equations, only 3 involve the variable y. All the others are func-

[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station. No. 31.

[2] Pearson, K., *Biometrika*, IV, 131–190. Cf. also Lewenz, M. A., and Pearson, K., *ibid.*, III, 367–397.

[3] Cf., for example, Pearl, R., Pepper, O. M., and Hagle, F. J., Carnegie Institution Publ. No. 58, 1907, and Donaldson, H. H., in *Jour. Comp. Neurol. and Psychol.*, XVIII, 345–392, 1908, and also in later papers.

tions of x. In practise many cases arise where all the base elements of the observational curve are *equal* and the values of x run in ordinal units from 1 to whatever number the observations comprise. In such cases, taking the origin of x at 0, the sums in (iii) which involve x and x^2 may be read off at once from Elderton's[4] tables of the sums of the powers of the natural numbers. If, now, similar tables are available from which one can obtain the values of $S(\log x)$, $S(x \log x)$ and $S(\log x)^2$ for integral values of x, there are left only the three sums in which y is involved which must be directly calculated.

So far as we are aware no tables have hitherto been published giving the sums of these logarithmic functions of the natural numbers. Consequently the present short table has been prepared. The immediate incentive to its calculation was the fact that in studies on growth and related topics in this laboratory it has been rather frequently necessary to fit these simple logarithmic curves. The table was calculated several years ago purely as a labor saving factor in the work of the laboratory. It has been used in manuscript here since that time. It seems desirable to publish it in order that other workers may have the benefit of the time and effort which it saves in curve-fitting work of this sort.

2. The values of $S(\log x)$, $S(x \log x)$ and $S(\log x)^2$ given in the appended table were calculated twice independently, once with 10-place values of the logarithms, and once with 7-place figures. The 10-place logarithms were taken from Vega's Thesaurus,[5] and the multiplications and summations were performed on a large size Brunsviga arithmometer. As was to be expected, the values of $S(x \log x)$ and $S(\log x)^2$ for the higher numbers, when calculated from 7-place logarithms, were not accurate beyond the fifth place. This 7-place table merely served as a rough check on the accuracy of the 10-place work. The tabled values given in this paper were all obtained by cutting off the last 3 figures from the values in the 10-place table. The accuracy of these last figures was previously tested by differences. The table as given is believed to be accurate in the seventh place. This is entirely sufficient because, as a matter of fact, in practical curve fitting work one will not ordinarily use more than 4 or at the most 5 places of figures in the logarithms.

[4] *Biometrika,* II, 474–480.

[5] For the loan of a copy of these tables we are greatly indebted to Dr. H. G. Kribs, of the University of Pennsylvania.

3. The use of the tables may be illustrated from a concrete example based on data collected in this laboratory. Each of the successively laid eggs of a certain hen were measured, length and breadth being recorded. From these records the length-breadth index (100 breadth ÷ length) was calculated. In all 87 eggs were measured.[6] To the line given by plotting the value of the index of each of these eggs in consecutive order as they were laid a curve of the type

$$y = a + bx + c(\log x)$$

was fitted by the method of least squares. In this equation y denotes the value of the length-breadth index of an egg whose ordinal number in the whole series laid is x. That is, $S(x)$ will be the sum of the integers from 1 to 87 inclusive.

The type equations for this curve have been given above (p. 756) and need not be repeated. For the data under discussion $n = 87$. From the table given in the present paper we read off at once

$$S \log x = 132.3238,$$
$$S(x \log x) = 6{,}602.9556,$$
$$S(\log x)^2 = 215.0293.$$

Further from Elderton's table (*loc. cit.*) we get

$$S(x) = 3{,}828,$$
$$S(x^2) = 223{,}300.$$

This leaves to be obtained by actual addition from the data *only*

$$S(y) = 5{,}473.81,$$
$$S(xy) = 245{,}041.55,$$
$$S(y \log x) = 8{,}416.4497.$$

Substituting these values in the type equation (iii) we have

$$87a + 3{,}828b + 132.3238c = 5{,}473.81,$$
$$3{,}828a + 223{,}300b + 6{,}602.9556c = 245{,}041.55,$$
$$132.3238a + 6{,}602.9556b + 215.0293c = 8{,}416.4497.$$

Solving

$$y = 49.0241 - .0910x + 11.7669 \log x.$$

The goodness of fit of this curve may be judged by examination of Plate II of the paper where the original data are published.[7]

[6] The actual measurements of these eggs are given in detail in the *Journal of Experimental Zoology*, VI, 349.

[7] *Jour. Exper. Zool., loc. cit.*

TABLE OF THE SUMS OF THE LOGARITHMS OF THE NATURAL NUMBERS FROM 1 TO 100

x	$S(\log x)$	$S(x \log x)$	$S(\log x)^2$
1	0.0000000	0.0000000	0.0000000
2	0.3010300	0.6020600	0.0906191
3	0.7781513	2.0334238	0.3182638
4	1.3802112	4.4416637	0.6807400
5	2.0791812	7.9365137	1.1692991
6	2.8573325	12.6054212	1.7748184
7	3.7024305	18.5211075	2.4890091
8	4.6055205	25.7458274	3.3045806
9	5.5597630	34.3340100	4.2151594
10	6.5597630	44.3340100	5.2151594
11	7.6011557	55.7893295	6.2996581
12	8.6803370	68.7395045	7.4642903
13	9.7942803	83.2207681	8.7051601
14	10.9404084	99.2665606	10.0187696
15	12.1164996	116.9079295	11.4019602
16	13.3206196	136.1738492	12.8518651
17	14.5510685	157.0914808	14.3658697
18	15.8063410	179.6863859	15.9415788
19	17.0850946	203.9827044	17.5767895
20	18.3861246	230.0033043	19.2694686
21	19.7083439	257.7699095	21.0177324
22	21.0507666	287.3032084	22.8198311
23	22.4124944	318.6229487	24.6741338
24	23.7927057	351.7480185	26.5791169
25	25.1906457	386.6965187	28.5333531
26	26.6056190	423.4858257	30.5355027
27	28.0369828	462.1326474	32.5843049
28	29.4841408	502.6530722	34.6785713
29	30.9465388	545.0626142	36.8171792
30	32.4236601	589.3762518	38.9990664
31	33.9150218	635.6084643	41.2232261
32	35.4201717	683.7732636	43.4887026
33	36.9386857	733.8842237	45.7945871
34	38.4701646	785.9545068	48.1400148
35	40.0142326	839.9968884	50.5241609
36	41.5705351	896.0237784	52.9462384
37	43.1387369	954.0472422	55.4054951
38	44.7185205	1,014.0790189	57.9012113
39	46.3095851	1,076.1305385	60.4326979
40	47.9116451	1,140.2129382	62.9992941
41	49.5244289	1,206.3370763	65.6003659
42	51.1476782	1,274.5135465	68.2353041
43	52.7811467	1,344.7526901	70.9035233
44	54.4245993	1,417.0646079	73.6044600
45	56.0778119	1,491.4591710	76.3375716
46	57.7405697	1,567.9460313	79.1023352
47	59.4126676	1,646.5346306	81.8982465
48	61.0939088	1,727.2342100	84.7248186
49	62.7841049	1,810.0538179	87.5815814
50	64.4830749	1,895.0023181	90.4680804

x	$S(\log x)$	$S(x \log x)$	$S(\log x)^2$
51	66.1906450	1,982.0883971	93.3838763
52	67.9066484	2,071.3205710	96.3285438
53	69.6309243	2,162.7071920	99.3016711
54	71.3633180	2,256.2564551	102.3028592
55	73.1036807	2,351.9764030	105.3317215
56	74.8518687	2,449.8749325	108.3878829
57	76.6077436	2,549.9597993	111.4709794
58	78.3711716	2,652.2386229	114.5806577
59	80.1420236	2,756.7188916	117.7165745
60	81.9201748	2,863.4079666	120.8783964
61	83.7055047	2,972.3130866	124.0657990
62	85.4978964	3,083.4413713	127.2784670
63	87.2972369	3,196.7998259	130.5160934
64	89.1034169	3,312.3953443	133.7783793
65	90.9163303	3,430.2347124	137.0650341
66	92.7358742	3,550.3246122	140.3757742
67	94.5619490	3,672.6716240	143.7103234
68	96.3944579	3,797.2822300	147.0684123
69	98.2333070	3,924.1628173	150.4497786
70	100.0784050	4,053.3196801	153.8541654
71	101.9296634	4,184.7590228	157.2813229
72	103.7869959	4,318.4869626	160.7310069
73	105.6503187	4,454.5095314	164.2029790
74	107.5195505	4,592.8326786	167.6970062
75	109.3946117	4,733.4622734	171.2128609
76	111.2754253	4,876.4041064	174.7503207
77	113.1619160	5,021.6638922	178.3091670
78	115.0540106	5,169.2472713	181.8891890
79	116.9516377	5,319.1598115	185.4901776
80	118.8547277	5,471.4070104	189.1119291
81	120.7632127	5,625.9942970	192.7542442
82	122.6770266	5,782.9270329	196.4169276
83	124.5961047	5,942.2105145	200.0997884
84	126.5203840	6,103.8499746	203.8026391
85	128.4498029	6,267.8505832	207.5252965
86	130.3843013	6,434.2174510	211.2675808
87	132.3238206	6,602.9556260	215.0293157
88	134.2683033	6,774.0701012	218.8103286
89	136.2176933	6,947.5658118	222.6104500
90	138.1719358	7,123.4476376	226.4295137
91	140.1309772	7,301.7204043	230.2673568
92	142.0947650	7,482.3888844	234.1238194
93	144.0632480	7,665.4577986	237.9987445
94	146.0363758	7,850.9318169	241.8919781
95	148.0140994	8,038.8155594	245.8033687
96	149.9963707	8,229.1135977	249.7327590
97	151.9831424	8,421.8304560	253.6800209
98	153.9743685	8,616.9706114	257.6450022
99	155.9700037	8,814.5384957	261.6275620
100	157.9700037	9,014.5384957	265.6275620

RAYMOND PEARL,
LOTTIE E. MCPHETERS.

NOTES AND LITERATURE

THE DOCTRINE OF EVOLUTION

In[1] "The Doctrine of Evolution," Professor Crampton is issuing in book form eight "Hewitt Lectures" delivered at Cooper Union in 1907 before "audiences made up almost exclusively of cultivated minds, but who were, on the whole, quite unfamiliar with the technical facts of natural history. . . . The course was, in a word, a simple message to the unscientific."

The scientific reader of this book, can not expect, then, to discover a new message in it for himself unless he be pretty woefully ignorant of all things connoted by the word evolution. And he will not. Or perhaps after all he will. For if he be a reader who relegates evolution to the world of lower creatures, the plants and "animals," he may find himself suddenly learning that he too is a part of evolution and nothing else besides. Because that is what this book teaches very strongly. Four of the eight chapters of it discuss the evolution of man; first, the evolution of his physical self, then of his mental self, then of his social and ethical self, and finally of all there is left of him, to wit, his religious, theological and philosophical self. It is this part of the book that as "a simple message to the unscientific" may make even a few scientific open wide eyes and be strongly attracted or repelled by it. For the treatment of man in all his parts and activities as a wholly natural, perfectly explicable and perhaps quite to be expected product of the great, world-dominating, blind *causa efficiens* that is evolution, has not been more lucidly, strongly and consistently done—that is, as far as my reading goes. This may, of course, say more about the limitations of my reading than of the quality of Professor Crampton's book; but that is the reader's risk with any reviewer.

Especially is Chapter VII, "Social Evolution as a Biological Process," well handled. There is more of a whole-souled sureness with less of an imitating dogmatism of language about the

[1] "The Doctrine of Evolution," by Henry Edward Crampton, professor of zoology in Columbia University, 311 pp., 1911, Columbia University Press, New York, $1.50.

treatment of social evolution in this concise chapter than one usually gets from others who consider this subject from the same point of view. The three laws of life that make social evolution possible and inevitable, viz., "Preserve thyself," "Preserve thy kind," "Remain together," and the course of biological and sociologic specialization, are all very happily exposed and illustrated.

In the chapter on "Evolution and the Higher Human Life," Professor Crampton has been admirably bold and explicit. His treatment is encouragingly specific. His consistent attitude as a thoroughgoing evolutionary explainer of man's body, mind and social life, receives no shadow of weakening from his attitude toward man's ethical, religious and philosophical capacities and activities. Man in the entirety of self and possession is a natural product, and evolution is his natural producer! That is the emphasized and conspicuous part of Professor Crampton's "simple message to the unscientific"! The rest of the book is really only preparation for this part of it.

V. L. K.

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